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SYSTEMATICS OF THE SUBFAMILY CLINOCARDIINAE KAFANOV, 1975 (BIVALVIA, CARDIIDAE)

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ABSTRACT

Revising the Cenozoic Cardioidea, the author has established the new subfamily Clinocardiinae. The history of studies of clinocardiines, the size and composition of the subfamily and its systematic position within the Cardiidae are considered. The paper presents keys to tribes, genera, species and subspecies, and detailed diagnoses for subfamily, tribes, genera and subgenera. The catalogue raisonné contains all the taxa of species rank (88) described until now with special notes on the original descriptions, type-localities and the depositories of the type materials. Necessary taxonomic remarks are given. For *Cardium pauperculum* Yokoyama, 1923 non Meek, 1871 a new name is suggested: *Serripes nodai* nom. nov.

Cardiidae are widely represented in Cenozoic marine deposits of the North Pacific and European Subarctic. For many stratigraphical subdivisions the representatives of this group are either zonal forms or the most characteristic species. They are also important in the identification of the Paleogene-Neogene boundary in the northwestern part of the Pacific mobile belt, and in the North Atlantic they are one of the most striking participants of the Neogene trans-Arctic migrations of the North Pacific molluscs.

Until recently almost all the diversity of North Pacific cardiids were assigned to only three genera: *Clinocardium* s.l., *Serripes* s.l. and *Papyridea* s.l. The revision made by the author (Kafanov, 1974a, b, 1975, 1976) has shown that some new taxa of generic rank and the new subfamily Clinocardiinae should be established for North Pacific Cardiidae.

The purpose of this paper is to review Recent and fossil Clinocardiinae. The taxonomic position of this subfamily within the Cenozoic Cardioidea Lamarck, 1809, is dealt with in detail in Kafanov & Popov (1977).

On the status of the subfamily Laevicardiinae Keen, 1936

When discussing the necessity for establishing a new genus for the North Pacific "*Cerastoderma,*" Keen (1936a) proposed the new subfamily Laevicardiinae. This subfamily includes forms which may be characterized by the following diagnosis (Keen, 1969: N589): "Elliptic-oblique; rib ornamentation of looped threads or small nodes, not spines; ribs of posterior slope weaker than those of central and anterior slopes or obsolescent; posterior margin wavy rather than notched; hinge long and arched (line joining laterals and cardinals bends more than 25 degrees); cardinal teeth somewhat unequal in size, anterior left lateral bladelike."

In this subfamily Keen (1951) originally included: *Laevicardium* Swainson, 1840 (with the subgenera *Laevicardium* s.s., *Fulvia* Gray, 1853 and *Dinocardium* Dall, 1900), *Serripes* Gould, 1841, *Cerastoderma* Poli, 1795 (with the subgenera *Cerastoderma* s.s., *Parvicardium* Monterosato, 1884), *Clinocardium* Keen, 1936, *Loxocardium* Cossmann, 1886 and *Plagiocardium* Cossmann, 1886 (with the subgenera *Plagiocardium* s.s., Maoricardium Marwick, 1944 and *Papillicardium* Sacco, 1899). In Keen's latest (1969) classification of the Cardioidea only the genera and subgenera *Laevicardium* s.s., *Laevicardium (Fulvia), Laevicardium (Dinocardium), Cerastoderma, Clinocardium* and *Serripes* are referred to the Laevicardiinae. More recently *Fulvia* has been raised to generic rank (Keen, 1973; Kafanov, 1974a).

Following Keen (1969), the author earlier adopted an identical interpretation of the Laevicardiinae (Kafanov, 1974a) but subdivided *Clinocardium* into *Clinocardium* s.s. and two new taxa, *Clinocardium (Keenocardium)* and *Ciliatocardium.* A year before, *Clinocardium (Fuscocardium)* was proposed by Oyama (1973). Glibert & van de Poel

(1970), however, consider the Laevicardiinae to include *Cerastoderma* together with the genus *Laevicardium* broadly understood by them and its four subgenera: *Laevicardium* s.s., *Dinocardium* s.s., *Clinocardium* and *Habecardium* Glibert & van de Poel, 1970. Popov (1977), taking into consideration Keen's (1950) remarks, considers the latter a subgenus of *Nemocardium* Meek, 1876.

More recently it has been found that the Laevicardiinae sensu Keen are polyphyletic (Kafanov, 1975; Popov, 1977; Kafanov & Popov, 1977). According to shell microstructure (Popov, 1977) and conchological features, its genera are subdivided into three different groups: 1) *Cerastoderma* closely related to *Acanthocardia* Gray, 1851 and *Parvicardium* on the one hand, and, on the other hand, to the Ponto-Caspian brackish-water Lymnocardiinae Stoliczka, 1870; 2) *Laevicardium* and *Fulvia* are similar to *Cardium* Linné, 1758, *Bucardium* Gray, 1853, *Vepricardium* Iredale, 1929 and *Trachycardium* Mörch, 1853 and other closely related genera; 3) *Clinocardium* s.l. and *Serripes* s.l. differed in their characteristic shell morphology and microstructure not observed in representatives of other cardiid genera, while *Dinocardium* has a microstructure rather similar to both genera above. *Clinocardium* s.l. and *Serripes* s.l. were assigned by the author (Kafanov, 1975) to the new subfamily Clinocardiinae. Together with the numerous features of morphological similarity, phylogenetic unity of the genera involved is also confirmed by the abundant paleontological data.

According to Keen (1936b), *Clinocardium* is most closely related to *Cerastoderma*, from which it differs by its prosogyrate beaks, its long, narrow and low ligament, its arched hinge margin and by its greater number of radial ribs. *Cerastoderma* and *Clinocardium* s.l., however, have different centres of origin (Kafanov, 1974a, 1975). *Cerastoderma* appeared in the Oligocene basins of the Eastern Paratethys, as is well documented by paleontological data (Merklin, 1974), but the early stages of the evolution of the Clinocardiinae occurred in the Northern Japan-Sakhalin Paleogene province. Therefore, some similar morphological peculiarities of these two groups really resulted from convergent development and do not indicate common origin.

The Lymnocardiinae in Keen's (1969) classification also is not a natural (monophyletic) taxon. Comparison of shell morphology in the numerous genera of the Ponto-Caspian brackish-water cardiids and the use of data on shell microstructure (Popov, 1973, 1977) convincingly confirm the view that the overwhelming majority of taxa of neolimnitic (sensu Martinson, 1958) genesis arose from *Cerastoderma*, namely from some lagoonal forms like the Recent extremely euryhaline *C. glaucum* (Poiret, 1789) (Eberzin, 1965, 1967; Starobogatov, 1970). The similarity of the general scheme of the stomach morphology (Starobogatov in Kafanov & Popov, 1977) and spermatozoids (Karpevich, 1961, 1964) in *Cerastoderma, Didacna* Eichwald, 1838 and *Hypanis* Menetries, 1832 affirm this origin unequivocally. However, the brackish-water cardiids and *Cerastoderma* are considered separate by Keen (1969): the former—to belong to the independent family Lymnocardiidae, the latter to the Laevicardiinae (Cardiidae s.s.).

Autochthony of the brackish-water faunas of the geological past almost unconnected genetically one with another and their relative short span of existence as compared with marine and fresh-water faunas have resulted in isolation from *Cerastoderma* of the brackish-water cardiids which occurred independently at different geological times. Similar structures, developed in parallel and asynchronously in different branches, recurred in new evolutionary lines (about eleven). This process determined the specific features of "supralimital specialization" (Myers, 1960) of the Ponto-Caspian groups of neolimnitic genesis. To the extent that the principle of the successive monophyly is the basis of construction for each natural system, *Cerastoderma* and the overwhelming majority of Ponto-Caspian brackish-water genera must be incorporated into one taxon of high rank (Kafanov, 1975; Popov, 1977; Kafanov & Popov, 1977). Only such a taxonomic interpretation shows the phylogenetic unity of all brackish-water cardiids. Hence, there is no place for *Cerastoderma* within the Laevicardiinae.

The taxonomic position of *Dinocardium* is the most mysterious. Shell configuration, costal ornamentation (transverse toruli or tubercula on the ridges) and the presence of the rudimentary external layer of the simple prismatic structure (Popov, 1977) resemble analogous characters in *Clinocardium*. However, it differs from the latter as follows (Fig. 1): 1) proximal end of the anterior part of hinge margin covers the anterior beak slope, frequently observed in *Laevicardium* and *Trachycardium*; 2) lunula formed by "lapel" of proximal end of the anterior part of hinge

margin, and from anterior preapical valve surface restricted by deep vallicula; 3) scars of the dorso-umbonal muscles were not found, and 4) ligament is considerably higher and shorter than in *Clinocardium* and *Serripes*. According to the author (Kafanov & Popov, 1977), it would be better to consider *Dinocardium* a member of the Cardiinae until additional data are obtained.

Only *Laevicardium* and *Fulvia,* therefore, remain in the Laevicardiinae. *Cerastoderma*, *Clinocardium* s.l., *Serripes* s.l. and *Dinocardium* are considered to be separate.

Clinocardiinae Kafanov, 1975

The subfamily Clinocardiinae represents a discrete natural group. *Clinocardium* s.l. and *Serripes* s.l. assigned to this subfamily are distinguished by a rare type of shell microstructure and in this character they are very different from the other genera of Cardiidae (Oberling, 1964; Popov, 1973, 1977).

Stewart (1930) and Keen (1936a) were the first to establish a new genus for a fairly numerous group of the North Pacific Recent and fossil species, previously referred by most authors to either *Cerastoderma* or *Laevicardium.* Stewart (1930) discusses in some detail the relationship of *Cardium nuttallii* Conrad, 1837 (= *Cardium corbis* auct. plur.) to *Dinocardium,* and he includes *Cerastoderma* s.s. and *Cerastoderma (Dinocardium)* in the subfamily Trachycardiinae established by him, taking note, however, of their considerable similarity with the Cardiinae. Keen (1936b) proposed a new genus *Clinocardium* (type-species *Cardium nuttallii* Conrad, 1837) and referred it to the Laevicardiinae which initially incorporated eleven species.

The name *Clinocardium* has been used in most hydrobiological and paleontological papers and has been commonly accepted. However, *Clinocardium* sensu Keen is a highly nonhomogeneous group from the morphological point of view. As long ago as 1934, Makiyama, in classifying the North Pacific Tertiary *"Cerastoderma,"* suggested the distinction of three groups of species including *Cardium decoratum* Grewingk, 1850 (nomen dubium, most probably included in *Clinocardium* s.s.), *Cardium californiense* Deshayes, 1839 and *Cardium ciliatum* Fabricius, 1780, according to the sculptural peculiarities of the external shell surface. Thus, the problem of the homogeneity of *Clinocardium* was discussed before a formal determination of the genus. Chinzei (1959) especially distinguished a group with ribs tri-

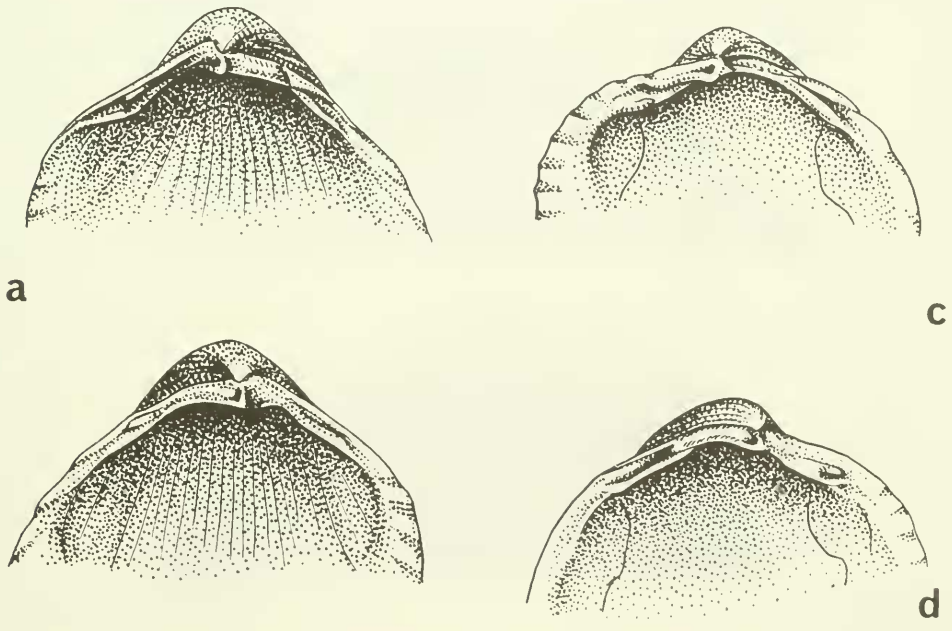

FIG. 1. Hinge structure in *Dinocardium robustum* (Lightfoot, 1768) (a–b) (Dinocardiini) and *Clinocardium nuttallii* (Conrad, 1837) (c–d) (Clinocardiini).

angular in cross section from Neogene Japanese *Clinocardium,* but Shuto (1960) emphasized that the majority of the *Clinocardium* representatives differed from type-species in the character of the radial ribs. The same author foresaw the possibility of separating some subgenera from the genus.

Analysis of the Recent and fossil forms assigned by Keen (1936b, 1954, 1973) to *Clinocardium* has shown that according to their morphological peculiarities and above all to the type of structure in transverse section of the radial ribs (Fig. 2) they form three taxa, separated by discontinuities, well differentiated from each other and representing the single phylogenetic lines which agree with the criteria for generic groups of Mayr (1971). These groups include the Recent *Cardium nuttallii, C. californiense* and *C. ciliatum,* respectively, which were designated the type-species for *Clinocardium* s.s., *Clinocardium (Keenocardium)* Kafanov, 1974 and *Ciliatocardium* Kafanov, 1974. In the present paper *Keenocardium* is raised to generic rank. The considerable morphological differences between *Clinocardium* s.s. and *Keenocardium,* various trends in their historical development and major changes of the adaptive zones of these two groups (Kafanov, unpublished) suggest the change in rank, as does the necessity of the taxonomic separation of *Clinocardium (Fuscocardium)* which is much

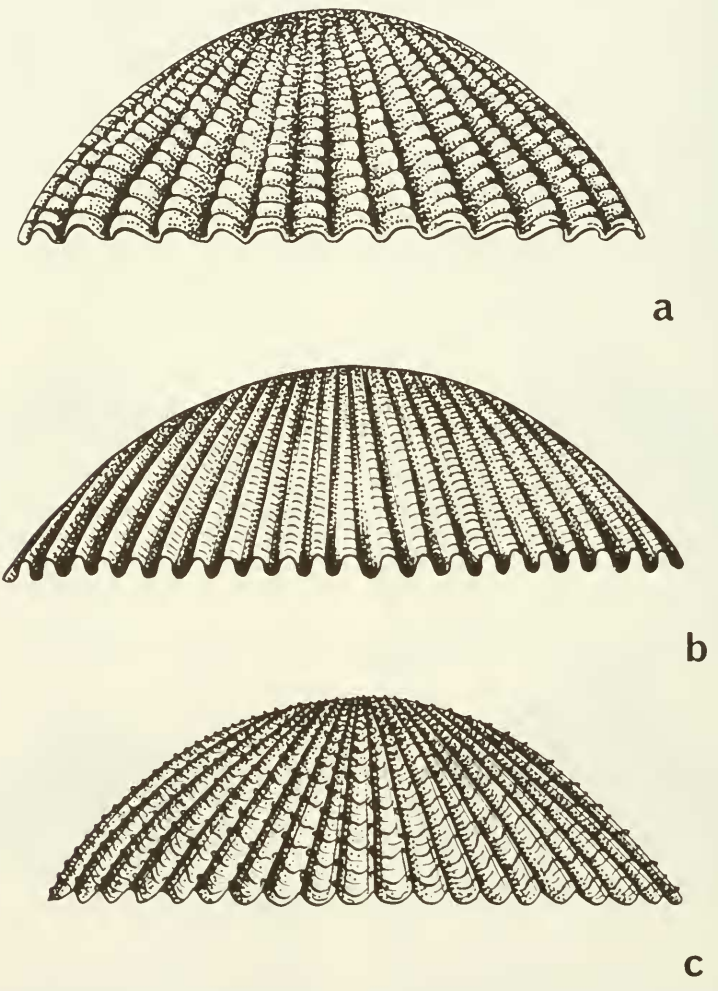

FIG. 2. Rib structure in *Clinocardium* (a), *Keenocardium* (b) and *Ciliatocardium* (c).

closer to *Clinocardium* s.s. than to *Keenocardium*. It should be emphasized that both conchological and anatomical differences (see key to the genera and diagnoses of the corresponding taxa) are the basis for subdivision of *Clinocardium* sensu Keen into three genera.

Similarly, the genus *Serripes* proves to be nonhomogeneous. At present among all the known species and subspecies five forms grouped around the Recent *Cardium (Serripes) notabile* Sowerby, 1915 perfectly form the isolated morphological and evolutionary lineages. The representatives of this group are distinguished by the carinate and markedly convex shells with narrow anterior margins, by strongly prosogyrate beaks, by more completely developed hinges, by the position and details of structure of anterior lower lateral teeth and also by topography of the rudimentary radial sculpture different from that of the typical *Serripes* (Fig. 3). For this group the author (Kafanov, 1975) erected a new genus *Yagudinella*.

Despite the definite morphological similarity of *Serripes, Yagudinella, Clinocardium* s.s., *Clinocardium (Fuscocardium), Keenocardium* and *Ciliatocardium,* the first two genera are more closely related to each other than to the other four, from which they differ in their strong reduction of the sculpture on the external valve surfaces and the less developed hinge. These differences enabled us to subdivide the Clinocardiinae into two tribes as follows: Clinocardiini and Serripedini (Kafanov, 1975), in perfect agreement with some internal shell structure as well (Popov, 1977).

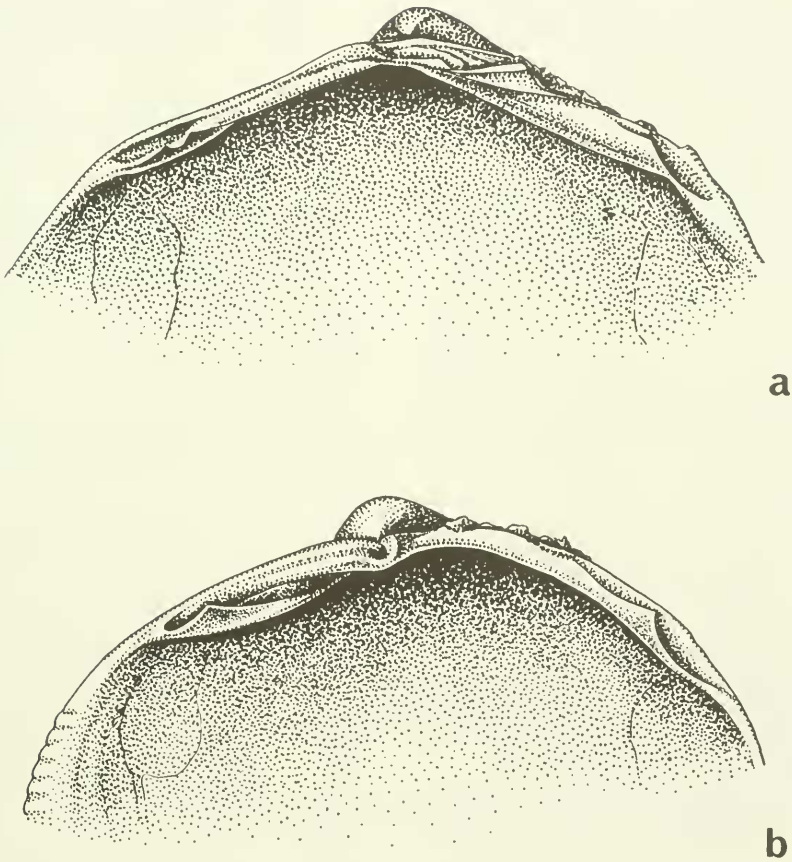

FIG. 3. Hinge structure in *Serripes groenlandicus* (Bruguière, 1789) (a) and *Yagudinella notabilis* (Sowerby, 1915) (b).

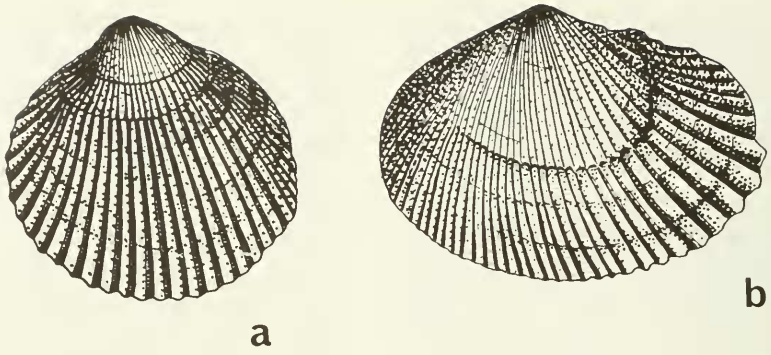

FIG. 4. Rib arrangement in Clinocardiini (a) and Profulviini (b).

The Far Eastern Tertiary *"Papyridea"* being extremely unusual and referred by the author (Kafanov, 1976) to the new genus *Profulvia* (type-species: *Papyridea harrimani* Dall, 1904), form the third tribus. The representatives of this tribus differ from the other Clinocardiinae by their carinate shells, anterior and posterior gapes, with nearly orthogyrate or slightly opisthogyrate apex and by the nature of the costae on the posterior valve surface: arched ribs with convexity anteriad while in the other Clinocardiinae the convexity is posteriad (Fig. 4).

The classification of the Clinocardiinae adopted in the present paper is the following one:

Family Cardiidae Lamarck, 1809

Subfamily Clinocardiinae Kafanov, 1975

Tribus *Clinocardiini* Kafanov, 1975
- Genus *Clinocardium* Keen, 1936
  - Subgenus *Clinocardium* Keen, 1936
  - Subgenus *Fuscocardium* Oyama, 1973
- Genus *Keenocardium* Kafanov, 1974 grad. nov.
- Genus *Ciliatocardium* Kafanov, 1974

Tribus Profulviini Kafanov in Kafanov & Popov, 1977[1]
- Genus *Profulvia* Kafanov, 1976

Tribus Serripedini Kafanov, 1975
- Genus *Serripes* Gould, 1841 (ex Beck, MS)
- Genus *Yagudinella* Kafanov, 1975

Key to the tribes, genera and subgenera of Clinocardiinae:

1. Radial ribs not reduced 2
   Radial ribs strongly or completely reduced 6
   (Serripedini Kafanov, 1975)
2. Carina nearly obsolete; shell without gapes; ribs on the posterior valve surfaces convex back (Fig. 4a) 3
   (Clinocardiini Kafanov, 1975)
   Shell carinate, gaping at the back or from both sides; ribs on posterior valve surfaces curved with convexity forward (Fig. 4b) . . . . . Profulviini Kafanov in Kafanov et Popov, 1977 (the monotypic tribus)
3. Ribs rounded, flattened or nearly rectangular in cross section, not placed on anterior valve surfaces; ridges of ribs with frequent transverse nodular tubercula or nearly smooth 4
   Ribs triangular or roof-like in cross section (Fig. 2c) and often widely extended on the anterior valve surfaces; ridges of ribs with longitudinal rows of thin ciliated periostracum fringes (in poorly preserved fossil shells ribs may be differently smoothed) . . . . . *Ciliatocardium* Kafanov, 1974
4. Beaks high; ribs about 20–40 in number; ridges of ribs with transverse nodular tubercula (Fig. 2a); labial palps short, about one-fourth length of the inner demibranch 5
   (*Clinocardium* Keen, 1936)

[1] "Profulviini Kafanov et Popov" as published with the original description is a typographical error.

Beaks low; ribs about 28–65 in number; nodular tubercula absent on ridges of ribs (Fig. 2b); labial palps relatively long but less than half the length of the inner demibranch ..... *Keenocardium* Kafanov, 1974

5. Intercostal interspaces appreciably narrower than ribs; ribs about 30–40 in number, flattened and rounded in cross section ..... *Clinocardium* s.s.
   Width of intercostal interspaces nearly equal to width of ribs; ribs about 20–30 in number, rectangular in cross section ..... *Clinocardium (Fuscocardium)* Oyama, 1973
6. Beaks moderately prosogyrate or nearly orthogyrate; rudiments of radial ribs mainly observed on the posterior valve surfaces; hinge strongly reduced, frequently teeth completely absent; bases of the anterior lower lateral teeth lie on outer side of the internal branches of hinge margin (Fig. 3a) ..... *Serripes* Gould, 1841 (ex Beck, MS)
   Bases obviously prosogyrate; rudiments of radial ribs largely presented on the anterior valve surfaces; hinge normal for Clinocardiinae; bases of the anterior lower lateral teeth tend to be on ventral side of the anterior branches of hinge margin, but their proximal parts elongated within the beaks (Fig. 3b) ..... *Yagudinella* Kafanov, 1975.

Composition of the Clinocardiinae Kafanov, 1975

At present about 73 valid taxa of specific and subspecific rank are referred to the Clinocardiinae; 5 taxa are provisionally referred to this subfamily. A complete list of them was lacking. Slodkewitsch (1938) gives the detailed review of the North Pacific Tertiary *"Papyridea."* Keen (1954) lists about 18 nominal species of *Clinocardium* s.l. and describes three new species from Neogene formations of northwestern America. Noda (1962) gives a systematic review of the Japanese *Serripes* s.l. Keen (1973) lists Far Eastern *Clinocardium* s.l., *Serripes* s.l. and *Fulvia* (including *Profulvia*). A list of Clinocardiini has previously been given by the author (Kafanov, 1974a). The known representatives of *Yagudinella* are also listed by Kafanov (1975). Finally, there is a very incomplete list of *Clinocardium* s.l. and *Serripes* s.l. in Popov's (1977) monograph.

The author excludes from the Clinocardiinae the following forms assigned by Keen (1973) to *Clinocardium* and *Serripes: Cardium annae* Pilsbry, 1904: 557, pl. 40, fig. 20; *Vasticardium arenicoloides* Akutsu, 1964: 284, pl. 59, figs. 6, 7; *Laevicardium (Cerastoderma) etheringtoni* Slodkewitsch, 1938 (ex Kogan, MS): 388, pl. 74, figs. 11, 11a, 12; *Cardium (Trachycardium) hanpeizanense* Nomura, 1933: 77, pl. 1, figs. 7, 8, pl. 2, figs. 8, 9; *Cardium (Cerastoderma) hanzawai* Nomura, 1933: 79, pl. 3, figs. 18, 19; *Cardium (Cerastoderma) hizenense* Nagao, 1928: 61(51), pl. 10, figs. 15–17; *Cardium coosense rhomboideum* Khomenko, 1934: 52, pl. 12, figs. 5, 6; *Vasticardium shimotokuraense* Akutsu, 1964: 283, pl. 59, figs. 9, 10. *Laevicardium (Cerastoderma) esutoruense* Krishtofovich, [1957]: 93, pl. 16, figs. 4, 5, 6, 6a, 8,13, mentioned by the author as *Keenocardium* (Kafanov, 1974: 1469) is *Laevicardium*.

Cardium (Laevicardium) jobanicum Yokoyama, 1924: 15, pl. 2, figs. 12–18 from the Oligocene Iwaki formation of the northeastern part of the Central Honshu included by Keen (1973) in *Clinocardium*, must be considered a member of the Veneridae, either *Protothaca* (Hatai & Nisiyama, 1952) or *Cyclina* Deshayes, 1849 non Gray, 1857 (Kamada, 1962).

Popov (1977) refers *Cardium gallicum* Mayer, 1866: 72, pl. 2, fig. 3 and *Cardium (Laevicardium) pantecolpatum* Cossmann & Peyrot, 1911: 517, pl. 23, figs. 32–35 from the Miocene of France, as well as *Cardium (Cerastoderma) scapoosense* Clark, 1925: 91, pl. 22, fig. 5 and *Cardium sookense* Clark & Arnold, 1923: 145, pl. 22, figs. 1a–b, 2 from the Oligocene of the Pacific coast of the North America to *Clinocardium*. The first two species have nothing in common with *Clinocardium* or with the Clinocardiinae in general. Generic relationship of the latter two forms is uncertain. The considerably shortened and strongly curved hinge margin, nearly orthogyrate beaks, cardinal teeth (with hypertrophied anterior tooth of the left valve in *C. sookense*) which are strong, straight and misplaced with respect to each other—all prevent us from assigning these two species to the Clinocardiini. It is noteworthy that Keen (1936b, 1954) does not mention either *C. scapoosense* and *C. sookense* as belonging to *Clinocardium*. One therefore should examine all the related groups to see whether one might be found with characters that would overlap.

Cardium (Trachycardium) kinsimarae Makiyama, 1934: 141, pl. 6, fig. 35 and *Cardium puchlense* Ilyina in Zhizhchenko, Korobkov, Krishtofovich & Eberzin, 1949: 144, pl.

28, figs. 6–8, mentioned as *Clinocardium* in Zhidkova et al. (1974) are also excluded from the subfamily. *Cardium taracaicum* Yokoyama, 1930: 414, pl. 77, figs. 1, 2, called *Clinocardium* in some papers (Makiyama, 1959; Zhidkova et al., 1974; Sinelnikova et al., 1976), the author, following Keen (1973), belongs in *Laevicardium* s.l.

Cardium hudsoniense Deshayes, 1855: 331, a possible holotype of which is figured by Fischer-Piette (1977: pl. 12, fig. 1), should be considered a *Parvicardium,* not as a *Corculum (Keenocardium).*

Diagnoses of the subfamily, tribes and taxa of the generic group, as well as annotated catalogue and keys of all known species and subspecies with indications of type-localities and depositories, are given below. Valid taxa of the specific group are emphasized with boldface in the text. Nomina nuda are not examined.

Subfamily Clinocardiinae Kafanov, 1975

Kafanov,1975: 146.

Shell medium-sized or fairly large (to 120 mm and more), from truncate-trigonal to oblong-elliptical or neary ovate. Valve height usually less than length ($H = 0{,}926 \cdot L^{0{,}995 \pm 0.013}$ for the whole subfamily). Beaks prosogyrate, nearly orthogyrate or slightly opisthogyrate. Radial ribs about 20–65 in number. Ribs flattened and rounded, tectate or triangular in cross-section; combinations of these types are possible. Ribs smooth or with transverse nodular tubercula (but never with scales) or decorated with longitudinal rows of thin ciliated periostracal fringes (Fig. 2a–c). When sculpture of the external shell surface is obsolete, traces of the radial ribs will be found on posterior or rarely anterior valve surfaces. Hinge often strongly reduced. Typically there are (Fig. 1c–d): paired anterior lateral, paired cardinal and single posterior lateral teeth in right valve; paired cardinal and single lateral teeth in left valve. Reduction of the hinge elements is more often provided by that of the anterior upper lateral tooth of the right valve and of cardinal teeth. Posterior lateral tooth of the left valve may be split into two branches in distal part. Lunula and area are weak or absent. Ligament is long, narrow and low. Shell three-layered; mesostracum with cross-lamellar structure, ectostracum isolated and formed by spinose prisms or thin vertical plates oriented perpendicular to valve surfaces.

Paleocene(?)-Eocene-Recent; cold and temperate waters of the Northern Hemisphere, Paleogene and Neogene deposits of the North Pacific, North Atlantic and Arctic (Figs. 5–10).

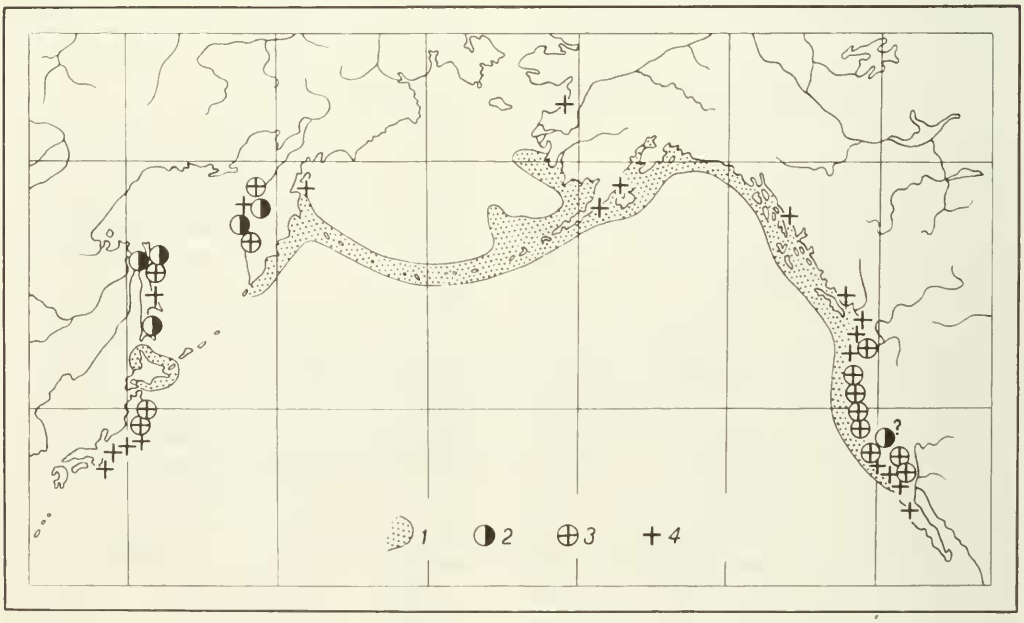

FIG. 5. Geographical and geological distribution of *Clinocardium*. 1—Recent; 2—Miocene; 3—Pliocene; 4—Pleistocene.

Tribus Clinocardiini Kafanov, 1975

Kafanov, 1975: 147.

Carina obsolete. Shell without gapes. Ribs well developed. Ribs on posterior part of valve posteriorly convex (Fig. 4a).

Geographical and geological distribution as in the subfamily.

Genus *Clinocardium* Keen, 1936

Clinocardium Keen, 1936b: 119; *Clinocardium (Clinocardium)* Keen: Kafanov, 1974a: 1468.

Type-species: *Cardium nuttallii* Conrad, 1837; Recent, off estuary of the Columbia River, Oregon, U.S.A. (original designation).

Shell medium-sized or large (to 100 mm and more), from flattened to fairly convex, oblong-elliptical or truncate-trigonal, inequilateral. Beaks high and prosogyrate. Ribs about 20–40 in number; ridges with transverse nodular tubercula sometimes slightly smoothed (Fig. 2b). Ribs flattened and rounded or rectangular in cross-section. Anterior lower lateral tooth of right valve with a small longitudinal ridge on dorsal surface. Lunula often well developed, lanceolate. Distal part of foot with narrow ventral sulculus surrounded on both sides by longitudinal rows of low papillae. Labial palps short, about one-fourth length of the internal demibranch.

Two subgenera—*Clinocardium* s.s. and *Clinocardium (Fuscocardium)* Oyama, 1973.

Middle Miocene-Recent; North Pacific (north to 60°N, south to Central Honshu and southern California, U.S.A.) (Fig. 5).

Subgenus *Clinocardium* Keen, 1936

Intercostal interspaces appreciably narrower than ribs. Ribs about 30–40 in number. Ribs flattened and rounded in cross-section; ridges with transverse nodular or tabular-shaped tubercula.

Geographical and geological distribution as in genus.

Key to the species and subspecies[2]

1. Average rib number about 34–35 ..... *nuttallii* (Conrad, 1837).
   Average rib number about 28–30 ..... 2.
2. Anterior margin of shell moderately narrower than their posterior margin ..... *meekianum meekianum* (Gabb, 1866).
   Anterior margin of shell much more narrower than their posterior margin ..... *meekianum myrae* Adegoke, 1969

Described taxa

californianum Conrad, 1837: 229, pl. 17, fig. 4 [*Cardium*]. Recent; vicinity of Santa Barbara, Califonia. Depository: unknown. Synonym of *Clinocardium (C.) nuttallii* (Conrad, 1837).

corbis auct. plur., non *Corbis* Martyn, 1784, Taf. 80; non-binom. (Official Index . . . , 1958: 11, Opinion 456). Synonym of *Clinocardium (C.) nuttallii* (Conrad, 1837).

? decoratum Grewingk, 1850: 347, pl. 4, figs. 3a–g [*Cardium*]. Unga Island, Alaska (type-locality here designated); "jüngsten Tertiärzeit" [Middle or Upper Miocene]. Depository: unknown. Due to the loss of the type material and inferiority of the original description and illustration *decoratum* must be considered a nomen dubium. Possible synonym of *Clinocardium (C.) nuttallii* (Conrad, 1837). Its taxonomic position will be considered in detail elsewhere (Kafanov, in press).

meekianum Gabb, 1866: 27, pl. 7, fig. 46 [*Cardium*]. Eagle Prairie, Humboldt County, California: Pliocene [Wildcat formation according to Keen & Bentson, 1944]. Depository (holotype): Academy of Natural Sciences of Philadelphia, Philadelphia, U.S.A., reg.no. 4497.

meekianum myrae Adegoke, 1969: 117, pl. 3, figs. 7, 9, pl. 7, fig. 6 (paratypes) [*Clinocardium*]. Kettleman Hills area, San Joaquin Valley, California; Etchegoin Formation, Lower Pliocene. For figure of holotype see Woodring et al., 1941: pl. 29, fig. 14. Depository (holotype): U.S. National Museum, Washington, U.S.A., reg. no. 495769.

? nanum Khomenko, 1931: 74, pl. 10, fig. 19 [*Cardium*]. Ekhabi, Okhinskij District, Eastern Sakhalin; Ekhabinskaya suite, Middle Miocene. Depository (holotype): Central Research geological prospecting Museum, Leningrad, USSR, reg. no. 28/3456. A juvenile specimen.

[2]Taxa conditionally included in the genus are not considered

nuttallii Conrad, 1837: 229, pl. 17, fig. 3 [*Cardium*]. Recent; "muddy salt marshes, a few miles from the estuary of the Columbia River," Oregon. Depository (lectotype): Academy of Natural Sciences of Philadelphia, Philadelphia, U.S.A., reg. no. 54036. Recent records: along the Pacific coast of North America from San Diego, California, to Nunivak Island; Aleutian, Pribiloff and Commander Islands; Eastern Kamchatka (north to Sivuchij Cape); northern Kurile Islands (Paramushir); Hokkaido (along the Pacific side to Hakodate). Fossil records: Ilyinskaya suite of Western Kamchatka (Middle Miocene), San Pablo Formation of California (Upper Miocene), Enemtenskaya suite of Western Kamchatka (Lower Pliocene), Pliocene Montesano, Empire and Quillayute formations of Oregon and Washington, Pliocene Purisima, Etchegoin and Falor formations of California, Pleistocene of Alaska, Aleutian Islands, Kamchatka, Sakhalin, Washington, Oregon and California.

Subgenus *Fuscocardium* Oyama, 1973

Clinocardium (Fuscocardium) Oyama, 1973: 100.

Type-species: *Cardium braunsi* Tokunaga, 1906; Pleistocene, environs of Tokyo, Japan (original designation).

Width of intercostal interspaces nearly equal to width of ribs. Ribs about 20–30 in number, rectangular in cross-section. Transverse tabular-shaped tubercula on crests or ribs smooth.

Middle Miocene-Pleistocene; Honshu, Sakhalin and Kamchatka.

Key to the species

Average number of ribs about 20–22 ..... *braunsi* (Tokunaga, 1906)
Average number of ribs about 27–30 ..... *pseudofastosum* (Nomura, 1937)

Described taxa

braunsi Tokunaga, 1906: 51, pl. 3, fig. 11 [*Cardium*]. Oji, near Tokyo; "Upper Musashino," Pleistocene. Possible depository: College of Sciences, University of Tokyo, Tokyo, Japan. Characteristic species in Pleistocene deposits of the Kanto region, Central Honshu (Katori, Sakishima, Atsumi, Uemachi, Takinokawa and Toshima formations) and Eastern Sakhalin ("Nadnutovskaya" suite). Unknown in the Recent.

? nomurai Hayasaka, 1956: 18, pl. 2, figs. 4a–b ["*Clinocardium.*"] Path side cutting at Onoda, Futaba District, Fukushima Prefecture, Honshu; Ishiguma formation, Pliocene, Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 77376. Assignment of a given species to this subgenus is very difficult because of poor preservation. Hayasaka (l.c.) compares it to *Clinocardium nuttallii* (Conrad, 1837). According to the author, however, the form described here is more closely related to *Clinocardium (Fuscocardium) braunsi* (Tokunaga, 1906).

ovata Yokoyama, 1922: 157, pl. 12, fig. 4 [*Cardium tokunagai* var.]. Shisui, Chiba Prefecture, Honshu; "Upper Musashino," Pleistocene. Depository: Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?. Synonym of *Clinocardium (Fuscocardium) braunsi* (Tokunaga, 1906).

pseudofastosum Nomura, 1937: 171, pl. 23, figs. 1 (holotype), 2 [*Cardium (Clinocardium)*]. Kitamata-gawa, along the upper course of Koromogawa, Isawa District, Iwate Prefecture, Honshu;[3] Yushima formation (Hatai & Nisiyama, 1952), Pliocene. Depository (holotype): Saito Ho-on Kai Museum, Sendai, Japan, reg. no. 2388. Very similar forms were reported from Ilyinskaya suite of western Kamchatka (Kafanov & Savitzky, in press).

tokunagai Yokoyama, 1922: 156, pl. 12, figs. 6 (lectotype; designated as holotype by Taki & Oyama, 1954: pl. 32), 5 [*Cardium*]. Otake, Chiba Prefecture, Honshu; "Upper Musashino," Pleistocene. Depository (lectotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?. Synonym of *Clinocardium (Fuscocardium) braunsi* (Tokunaga, 1906). Following Taki & Oyama (Taki & Omaya, 1954; Oyama, 1973) who saw Yokoyama's materials, the author con-

[3]For detailed type-localities of Japanese species (Paleogene and Neogene) described prior to 1952 see Hatai & Nisiyama, 1952.

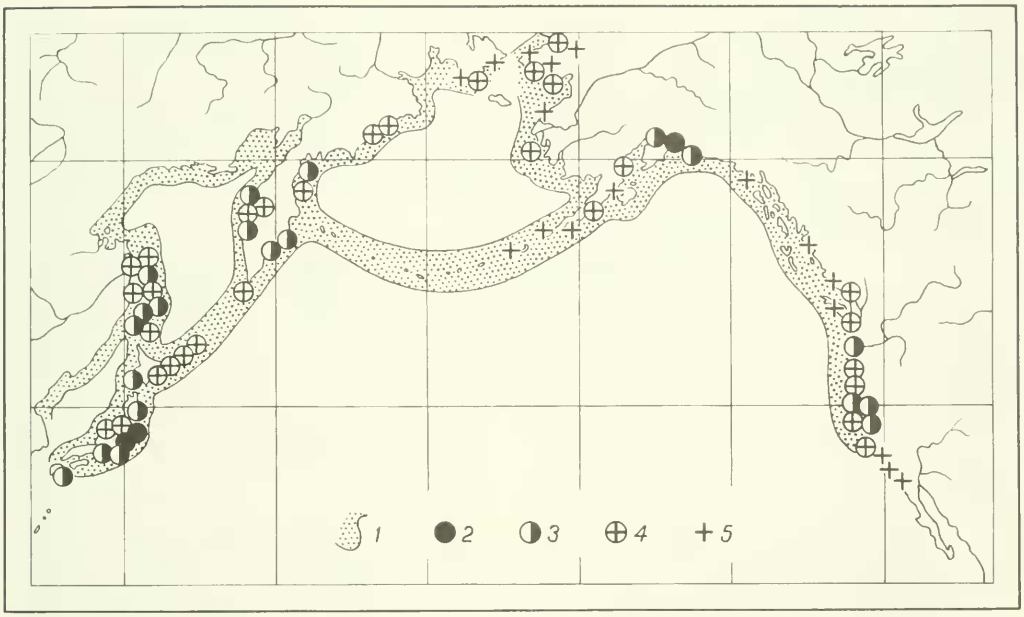

FIG. 6. Geographical and geological distribution of *Keenocardium*. 1—Recent; 2—Oligocene; 3—Miocene; 4—Pliocene; 5—Pleistocene.

siders *C. tokunagai* and *C. tokunagai* var. *ovata* to be *Clinocardium (Fuscocardium) braunsi* (Tokunaga, 1906).

Genus *Keenocardium* Kafanov, 1974

Clinocardium (Keenocardium) Kafanov, 1974a: 1468.

Type-species: *Cardium californiense* Deshayes, 1839; Recent, [Eastern] Kamchatka (original designation).

Shell medium-sized (to 80 mm and more), elongated and rounded or oval-trigonal, inequilateral, slightly convex. Beaks only weakly prosogyrate, displaced somewhat forward, narrow, slightly elevated. Ribs about 28–65 in number, rounded or flattened and rounded in cross-section, separated by narrower intercostal spaces; ribs, as a rule, closely set on anterior part of valve. Costal surfaces smooth, interrupted by narrow concentric wrinkles only. Anterior lower lateral tooth of right valve frequently with a small longitudinal ridge on dorsal surface. No lunula and escutcheon. Distal part of foot with narrower ventral sulculus surrounded on both sides by smoothed magins. Labial palps long but less than a half the length of the inner demibranch.

Early Oligocene—Recent; North Pacific (southern to Korea, Northwestern Kyushu and southern California), Bering Strait and Northwestern Alaska (Fig. 6).

Key to the species and subspecies

1. Ribs of posterior area crowded and crumpled into an irregular channel ..... 2.
   Ribs of posterior area not forming an irregular channel ..... 3.
2. Average rib number about 44–46 ..... *californiense californiense* (Deshayes, 1839).
   Average rib number about 49–51 ..... *californiense uchidai* (Habe, 1955).
3. Shell ovate, rounded, orbicular, suborbicular or semi-quadrate in outline; posterior dorsal margin not sloping obliquely downward ..... 4.
   Shell trigonal in outline; posterior dorsal margin sloping obliquely downward ..... 13.
4. Maximum size of adult shell more than 40 mm ..... 5.
   Maximum size of adult shell fewer than 40 mm ..... 7.

5. Shell strongly inequilateral (beaks near the anterior 0,35–0,37); ribs 30–33 ..... *iwasiroense* (Nomura, 1935).
   Shell subequilateral (beaks near the anterior 0,42–0,45); ribs 44–60 ..... 6.
6. Height of shell less than length (average height/length ratio about 0,94–0,95); ribs 50–60 separated by much narrower interspaces ..... *fastosum* (Yokoyama, 1927).
   Height of shell nearly equal to length (average height/length ratio about 1,00); ribs 44–49 sepated by somewhat narrower interspaces ..... *coosense* (Dall, 1909).
7. Ribs 45 or more ..... 8.
   Ribs fewer than 45 ..... 10.
8. Shell semi-quadrate in outline; interspaces about equal to the width of the ribs ..... *okushirense* (Uozumi & Fujie, 1966).
   Shell ovate or suborbicular in outline; interspaces somewhat narrower than the width of the ribs ..... 9.
9. Shell subequilateral (beaks near the anterior 0,43); average height/length ratio about 0,86–0,87 ..... *fucanum* (Dall, 1907).
   Shell inequilateral (beaks near the anterior 0,38); average height/length ratio about 0,95–0,96 ..... *subdecussatum* (Shuto, 1960).
10. Ribs 38 or fewer ..... 11.
    Ribs 39–44 ..... 12.
11. Average height/length ratio about 0,96; interspaces narrower than the width of the ribs ..... *andoi* (Itoigawa & Shibata, 1975).
    Average height/length ratio about 0,86; interspaces about equal to the width of the ribs or even somewhat broader ..... *kljutschiense* (Krishtofovich, 1969).
12. Shell equilateral (beaks near the anterior 0,49) ..... *blandum* (Gould, 1850).
    Shell subequilateral (beaks near the anterior 0,44) ..... *arakawae* (Kamada, 1962).
13. Maximum size of adult shell more than 45 mm ..... 14.
    Maximum size of adult shell less than 45 mm ..... 16.
14. Ribs fewer than 40; interspaces about equal to the width of the ribs . *buelowi* (Rolle, 1896).
    Ribs more than 40; interspaces much narrower than the width of the ribs ..... 15.
15. Ribs 42–48 ..... *pristinum* (Keen, 1954).
    Ribs 60–65 ..... *lispum* (Roth & Talmadge, 1975).
16. Ribs about 55 in number ..... *hopkinsi* (Kanno, 1971).
    Ribs 35–40 ..... 17.
17. Average height/length ratio about 1,00 ..... *hannibali* (Keen, 1954).
    Average height/length ratio about 0,96 ..... *praeblandum* (Keen, 1954).

Described taxa

andoi Itoigawa & Shibata, 1975: 24, pl. 7, figs. 9a–b (holotype), pl. 8, figs.1–4 [*Clinocardium*]. Togari-ST, Akeyo-cho, Mizunami City, Gifu Prefecture, Honshu; Mizunami Group, Yamanouchi member, Miocene. Depository (holotype): Mizunami Fossil Museum, Mizunami City, Japan, reg. no. 10029.

arakawae Kamada, 1962: 105, pl. 10, figs. 15 (holotype), 16, 17 [*Clinocardium asagaiense arakawae*]. Mukaida, Yumotomachi, Joban City, Joban coal-field, Honshu; Asagai Formation, Oligocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 79383. For taxonomic notes see: Kafanov, 1974a: 1470.

blandum Gould, 1850: 276; 1852: 418; 1861: 14, pl. 36, figs. 534, 534a [*Cardium*]. Recent; Puget-Sound, Washington. Depository (lectotype): U.S. National Museum, Washington, D.C., U.S.A., reg. no. 3899. For figure of lectotype see: Schenck & Keen, 1940: pl. 2, figs. 17–20; Schenck, 1945: pl. 67, figs. 18–21.

boreale Broderip & Sowerby, 1829: 368 non Reeve, 1845, sp. 131, pl. 22 [*Cardium*]. Recent (?); Ice-Cape, Arctic coast of Alaska. Depository: unknown. Nomen oblitum presented to International Commission on Zoological Nomenclature for inclusion in Official Index of rejected and invalid names in zoological nomenclature (Kafanov, 1974b; see also: Mayr & Melville, 1976). Synonym of *Keenocardium californiense* (Deshayes, 1839).

brooksi MacNeil in MacNeil, Mertie & Pilsbry, 1943: 91, pl. 15, fig. 14 [*Cardium (Cerastoderma) ciliatum brooksi*] non Clark, 1943: 812, pl. 18, fig. 5 [*Cardium (Papyridea)*]. Intermediate Beach, between Center

and Bourbon Creeks, near Nome, Alaska; Anvillian Pleistocene. Depository (holotype): U.S. National Museum, Washington, D.C., U.S.A., reg. no. 499085. Synonym of *Keenocardium californiense* (Deshayes, 1839).

buelowi Rolle, 1896: 114, pl. fig. C [*Cardium*]. Recent; Yokohama, Honshu. Depository (possible syntypes): Museum für Naturkunde, Humboldt-Universität, Berlin, G.D.R.

californiense Deshayes, 1839: 360; 1841a, pl. 47 (nom. conserv. propos., see: Kafanov, 1974b) [*Cardium*]. Recent; [Eastern] Kamchatka (here limited: in 1836 the region of investigations conducted by the French expedition on "Venus" near Kamchatka visited only the eastern coast and the lectotype is derived from those materials; Deshayes in the original description mentions this species form "Côtes de Californie" where it is absent). Depository (lectotype): Muséum National d'Histoire Naturelle, Paris, France, reg. no. ?. Recent records: Korea, northern and central Honshu (along the Pacific coast to Boso Peninsula, along the Sea of Japan coast to Noto Peninsula, Hokkaido, South Primorje, Sakhalin, Kurile Islands, Sea of Okhotsk, Kamchatka, Commander and Aleutian Islands, Southern Chukotka; along the Pacific coast of North America southward to Sitka Island, Alaska, and Vancouver Island (?), British Columbia. Fossil records: Kakertskaya and Etolonskaya suites of Kamchatka (Middle Miocene), lower and middle parts of Maruyamakaya suite of Sakhalin (Middle and Upper Miocene), Miocene Utsutoge, Hitosao and Gobansoyama formations of Honshu, lower part of Limimtevayamskaya suite of Karaginskij Island (Upper Miocene or Lower Pliocene), Empire Formation of Oregon (Lower Pliocene), upper part of Limimtevayamskaya and Ustj-Limimtevayamaskaya suites of Karaginskij Island (Pliocene), Nutovskaya, Uranajskaya, Ekhabinskaya, Pomyrskaya and upper part of Maruyamskaya suites of Sakhalin (Pliocene), Pliocene Setana formation of Hokkaido and Kotari formation of Honshu, Beringian strata and their equivalents of Alaska (Upper Pliocene), Pleistocene of Pribiloff Islands, Chukotka, Koryak Plateau, Kamchatka, Kurile Islands, Sakkalin and North Japan.

coosense Dall, 1909: 118, pl. 13, figs. 3, 4 [*Cardium (Cerastoderma)*]. Coos Bay, Oregon; Empire formation, Lower Pliocene. Depository (holotype): U.S. National Museum, Washington, D.C., U.S.A., reg. no. 153933.

fastosum Yokoyama, 1927a: 178, pl. 48, fig. 5 [*Cardium*]. Kanazawa, Nagaya, Kosakamura, Kahoku District, Ishikawa Prefecture, Honshu; Onma formation, Lower Pliocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?. Makiyama (1959) referring to the personal communication of T. Kuroda, considers this species a synonym of *Keenocardium californiense* (Deshayes, 1839). This assignment is incorrect.

fucanum Dall, 1907: 112 [*Cardium*]. Recent; Juan-de-Fuca Strait, Puget-Sound, Washington. Depository (holotype): U.S. National Museum, Washington, D.C., U.S.A., reg. no. 427773. For figure of holotype see: Schenck & Keen, 1940: pl. 2, figs. 21–24; Schenck, 1945: pl. 67, figs. 22–25.

hannibali Keen, 1954: 18, pl. 1, fig. 16 (holotype), text-fig. 9 [*Clinocardium*]. Chehalis and Summit Sts., Aberdeen, Washington; Montesano formation, Lower Pliocene. Depository (holotype): Stanford University, Paleo. Type collection, Stanford, U.S.A., reg. no. 8302.

hopkinsi Kanno, 1971: 68, pl. 5, figs. 7 (holotype), 6a–b [*Clinocardium*]. Near the head of the Gulf of Alaska; upper part of the Poul Creek formation, Lower Miocene(?). Depository (holotype): Tokyo University of Education, Tokyo, Japan, reg. no. 8434.

interrogatorium Fischer-Piette, 1977: 21, pl. 2, fig. 2 [*Laevicardium*]. Recent; "Californie." Depository (holotype): Muséum National d'Histoire Naturelle, Paris, France, reg. no. ?. A juvenile specimen. It is possible that the type-locality is given erroneously. Synonym of *Keenocardium californiense* (Deshayes, 1839).

iwasiroense Nomura, 1935: 113, pl. 6, figs. 1, 2 (holotype not designated) [*Cardium (Cerastoderma)*]. Hitosao, Ogino District along the Agano-gawa, Fukushima Prefecture, Honshu; Hitosao Formation, Upper Miocene. Depository (holotype): Saito Ho-on Kai Museum, Sendai, Japan, reg. no. 2146.

kljutschiense Krishtofovich, 1969: 191, pl. 4, figs. 1 (holotype), 2, 3 [*Clinocardium*]. Goryachie Kljuchi, Tjushevskaya River, Kronotskij District, Eastern Kamchatka; "Goryachikh Kljuchej" suite, Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R. reg. no. 59/6780.

lispum Roth & Talmadge, 1975: 3, text-fig. 1a (holotype), 1b [*Clinocardium*]. Off the U.S. Highway 101 bridge over Eel River, Humboldt County, California; Rio Dell formation, Plio-

cene. Depository (holotype): Museum of Paleontology, University of California, Berkeley, U.S.A., reg. no. 14152.

okushirense Uozumi & Fujie, 1966: 150, pl. 12, figs. 4 (holotype), 5, 6 [*Clinocardium*]. Cliff along the river, about 400 m upper stream from the Miyatsu-gawa, Miyatsu, Okushiri Island, Southwest Hokkaido; Tsurikake Formation, Miocene. Depository (holotype): University of Hokkaido, Sapporo, Japan, reg. no. 13732.

praeblandum Keen, 1954: 15, pl. 1, figs. 6 (holotype), 1, text-figs. 5–6 [*Clinocardium*]. West end of Las Trampas Ridge near Walnut Creek, Concord Quadrangle, Contra Costa County, California; Briones formation, Upper Miocene. Depository (holotype): Museum of Paleontology, University of California, Berkeley, U.S.A., reg. no. 14836.

pristinum Keen, 1954: 16, pl. 1, figs. 15 (holotype), 9, text-figs. 7 (holotype), 8 [*Clinocardium*]. Southwest part of Shell Ridge, near Walnut Creek, Concord Quadrangle, Contra Costa County, California; San Pablo group, Neroly Formation (?), Upper Miocene. Depository (holotype): Museum of Paleontology, University of California, Berkeley, U.S.A., reg. no. 14838.

pseudofossile Reeve, 1845, sp. 52, pl. 10 [*Cardium*]. Recent; [Kamchatka] (type-locality here designated). Depository (syntypes): British Museum (Natural History), London, Great Britain, reg. no. 1975617. Synonym of *Keenocardium californiense* (Deshayes, 1839).

subdecussatum Shuto, 1960: 216, pl. 25, figs. 12 (holotype), 9, 10, 20, text-fig. 1c [*Clinocardium*]. Yamaji, Mino-mura, Koyu District, Miyazaki Prefecture; Kyushu; Miyazaki group, the lowest part of the Tsuma member, Upper Miocene. Depository (holotype): Department of Geology, Faculty of Sciences, Kyushu University, Fukuoka, Japan, reg. no. 4777.

californiense uchidai Habe, 1955: 11, pl. 2, figs. 5, 6 *[Clinocardium uchidai].* Recent; Akkeshi Bay, Hokkaido. Depository (holotype): National Science Museum, Tokyo, Japan, reg. no. 53378. This form name was first published by Kira (1954: 111, pl. 55, fig. 1), where "*Clinocardium uchidai* Habe, MS" was illustrated without a formal description; Kira's specific name is therefore a nomen nudum.

vulva Jousseaume, 1898: 81 [*Cardium*]. Recent; "Japon." Depository (holotype): Muséum National d'Histoire Naturelle, Paris, France, reg. no. ?. Synonym of *Keenocardium californiense* (Deshayes, 1839) fide Fischer-Piette, 1977, pl. 11, fig. 4.

Genus *Ciliatocardium* Kafanov, 1974

Ciliatocardium Kafanov, 1974a: 1469.

Type-species: *Cardium ciliatum* Fabricius, 1780: Recent, Greenland (original designation).

Shell medium-sized (to 80 mm and more), oval-rounded or truncated-trigonal, inequilateral, moderately inflated. Beaks fairly high, prosogyrate, elevated and curved. Ribs about 20–50 in number, often widely arranged on the anterior valve surfaces. Ribs triangular or tectate in cross-section. Crests of ribs with longitudinal rows of thin ciliated periostracal fringes (in poorly preserved fossil shells ribs may be differently smoothed); small spiniform (lobes) observed sometimes in juveniles on crests of ribs. Anterior lower lateral tooth of the right valve without longitudinal ridge on dorsal surface. Lunula oblong and cordiform or absent. Area if present narrow and lanceolate. Distal part of foot with narrow ventral sulculus surrounded on both sides by longitudinal rows of delicate papillae. Labial palps long but less than a half the length of the inner demibranch.

Paleocene(?)-Eocene-Recent; northwestern (south to Kyushu) and northeastern Pacific (south to Washington). Arctic and North Atlantic (south to Cape Cod, Iceland and southern Norway; in Pliocene south to England) (Fig. 7).

Key to the species and subspecies

1. Height of shell equal to or greater than length ..... 2.
   Height of shell less than length ..... 5.
2. Average rib number 30 or more than 30 ..... 3.
   Average rib number fewer than 30 ..... 4.
3. Shell inequilateral (beaks near the anterior 0,40–0,41), somewhat oblique ..... *ciliatum dawsoni* (Stimpson, 1863).
   Shell subequilateral (beaks near the anterior 0,44–0,45), not oblique ..... *yakatagense* (Clark, 1932).
4. Maximum size of adult shell more than 25 mm; shell trigonally ovate; average rib number about 26 ..... *hataii* (Hayasaka, 1956).

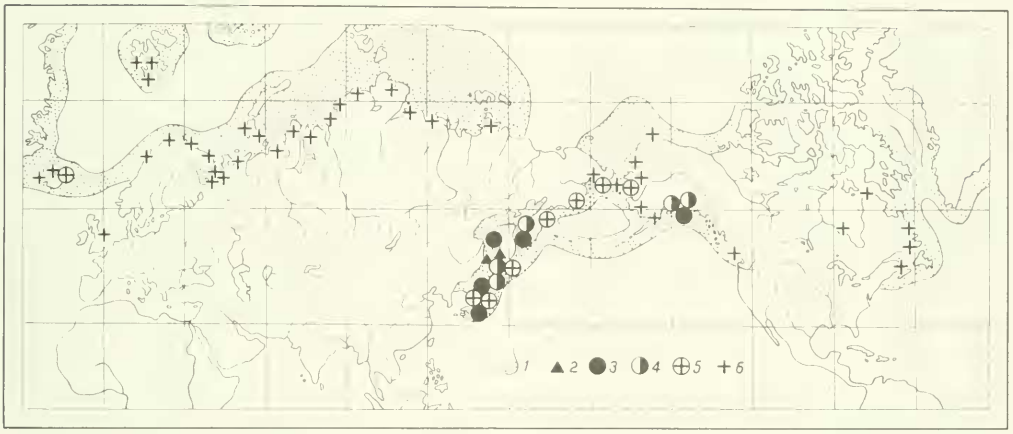

FIG. 7. Geographical and geological distribution of *Ciliatocardium*. 1—Recent; 2—Palaeocene and Eocene; 3—Oligocene; 4—Miocene; 5—Pliocene; 6—Pleistocene.

Maximum size of adult shell fewer than 25 mm; shell rounded; average rib number about 28 ..... *tigilense* (Slodkewitsch, 1938).

5. Average rib number 30 or more ..... 6.
   Average rib number fewer than 30 ..... 14.
6. Average height/length ratio more than 0,86 ..... 7.
   Average height/length ratio less than 0,85 ..... 12.
7. Maximum size of adult shell more than 45 mm ..... 8.
   Maximum size of adult shell less than 45 mm ..... 10.
8. Average height/length ratio about 0,96; shell rather inequilateral ..... *ciliatum ciliatum* (Fabricius, 1780).
   Average height/length ratio about 0,98; shell subequilateral or equilateral ..... 9.
9. Shell subequilateral (beaks near the anterior 0,44–0,45) ..... *ciliatum chikagawaense* (Kotaka, 1950).
   Shell equilateral (beaks near the anterior 0,48–0,49) ..... *ciliatum pubescens* (Couthouy, 1838).
10. Average height/length ratio about 0,91–0,92 ..... *asagaiense* (Makiyama, 1934).
    Average height/length ratio more than 0,94 ..... 11.
11. Average rib number about 40 ..... *ainuanum* (Yokoyama, 1927).
    Average rib number about 35 ..... *shinjiense* (Yokoyama, 1923).
12. Ribs 40 or more in number ..... *ermanensis* (Sinelnikova, 1976).
    Ribs 30–35 in number ..... 13.
13. Maximum size of adult shell more than 50 mm; average height/length ratio about 0,84 ..... *iwatense* (Chinzei, 1959).
    Maximum size of adult shell less than 50 mm; average height/length ratio about 0.81 ..... *schmidti* (Khramova, 1962).
14. Average height/length ratio 0,90 or more ..... 15.
    Average height/length ratio less than 0,90 ..... 17.
15. Maximum size of adult shell less than 40 mm ..... *yamasakii* (Makiyama, 1934).
    Maximum size of adult shell more than 40 mm ..... 16.
16. Ribs about 28 in number ..... *makiyamae* (Kamada, 1962).
    Ribs about 22–25 in number ..... *matchgarense* (Makiyama, 1934).
17. Maximum size of adult shell more than 40 mm ..... *uyemurai* (Kanehara, 1937).
    Maximum size of adult shell less than 40 mm ..... 18.
18. Average height/length ratio about 0,83–0,84; maximum size of adult shell about 36 mm ..... *mutuense* (Nomura & Hatai, 1936).
    Average height/length ratio about 0,86; maximum size of adult shell about 15 mm ..... *snatolense* (Krishtofovich, 1947).

Described taxa

ainuanum Yokoyama, 1927b: 202, pl. 51, figs. 7 (lectotype; designated by Hatai & Nisiyama, 1952: 35), 5, 6 [*Cardium*]. Sankebetsu, Haboromachi, Tomamae District, Teshio Province, Hokkaido; Haboro Formation, Lower or Middle Miocene. Depository (lectotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?.

arcticum Sowerby, 1841a: 106; 1841b: 2, no. 27, fig. 26 [*Cardium*]. Recent; "Arctic Seas." Depository (possible syntypes): British Museum (Natural History), London, Great Britain, reg. no. 1975618. Synonym of *Ciliatocardium ciliatum* (Fabricius, 1780).

asagaiense Makiyama, 1934: 139, pl. 5, figs. 23 (holotype), 20, 22 [*Cardium (Cerastoderma)*]. Taira, Yotsukura, Iwaki District, Fukushima Prefecture, Honshu; Shiramizu group, Asagai Formation, Oligocene. Depository (holotype): Institute of Geology and Mineralogy, Kyoto University, Kyoto, Japan, reg. no. 350011.

? brooksi Clark, 1932: 812, pl. 18, fig. 5 [*Cardium (Papyridea)*] non MacNeil in MacNeil, Mertie & Pilsbry, 1943: 91, pl. 15, fig. 14 [*Cardium (Cerastoderma)*]. Yakataga District (about 60°N), Gulf of Alaska; Poul Creek Formation, Upper Oligocene-Lower Miocene. Depository (holotype): Museum of Paleontology, University of California, Berkeley, U.S.A., reg. no. 30402.

ciliatum chikagawaense Kotaka, 1950: 46, pl. 5, figs. 1, 2, 5 (holotype), 3, 4, 6 [*Clinocardium chikagawaense*]. The sea cliff at the outlet of Chikagawa River at Chikagawa, Tanabu-machi, Shimokita District, Aomori Prefecture, Honshu; Hamada Formation, Pliocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 72999.

ciliatum Fabricius, 1790: 410 [*Cardium*]. Recent; Greenland [possibly southwestern coast]. Depository (lectotype: here designated): Universitetets Zoologiske Museum, Kϕbenhavn, Denmark, reg. no. ?. Recent records: North Pacific (south to Korea, Hokkaido, Boso Peninsula, Honshu, Aleutian and Commander Islands and Puget Sound, Washington), North Atlantic (south to southern Norway, south Iceland, south Greenland and Cape Cod, Massachusetts) and Arctic Seas. (Fig. 7). Fossil records: lower part of Maruyamskaya suite of Sakhalin (Middle Miocene), Komeutiyamskaya suite to Koryak Plateau (Upper Miocene), Utsutoge Formation of Honshu (Upper Miocene), Okobykajskaya suite of Northern Sakhalin (Upper Miocene), upper part of Limimtevayamskaya and Ustj-Limimtevayamskaya suites of Karaginskij Island (Pliocene), Alekhinskaya and Kamujskaya suites of Kurile Islands (Upper Miocene), Pliocene Golovinskaya suite of Kurile Islands, Setana Formation of Hokkaido, Kubo, Sawane and Shigarami formations of Honshu, Beringian Pliocene of Alaska and Pribiloff Islands, Upper Pliocene and Pleistocene of Iceland (Tjornes Crag, zone of *Serripes groenlandicus*), Chukotka (Pinakuljskaya suite), Iceland (Furuvik and Brejdavik), England (Icenian Crag) and Petchora Lowland (Kolvinskaya suite). One of the most widely distributed species in Quaternary deposits of Arctic and Subarctic.

comoxense Dall, 1900: 1093 [*Cardium*]. Vancouver Island, British Columbia; Pleistocene. Depository (lectotype): U.S. National Museum, Washington, D.C., U.S.A., reg. no. 427772. For figure of lectotype see: Keen, 1954: pl. 1, figs. 5, 7, 8. Synonym of *Ciliatocardium* ciliatum (Fabricius, 1780).

ciliatum dawsoni Stimpson, 1863: 58, text-fig. [*Cardium dawsoni*]. Hope Cape, southeastern coast of Hudson Bay, Canada; Pleistocene (?). Depository: unknown.

ermanensis Sinelnikova in Sinelnikova, Fotjanova, Chelebaeva et al., 1976: 38, pl. 6, fig. 18, 1 [*Clinocardium*]. Near Enemten Rocks, Tigiljskij District, western Kamchatka; the lowest part of Ermanovskaya suite, Upper Miocene. Depository (holotype): Geological Institute of the U.S.S.R. Academy of Sciences, Moscow, U.S.S.R., reg. no. 366/388.

hataii Hayasaka, 1956: 18, pl. 2, figs. 3a–b [*Clinocardium*]. Cliff of the Takesegawa River west of Takakura, Futaba District, Fukushima. Prefecture, Honshu; Ishiguma Formation, Pliocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 77375.

hayesii Stimpson, 1864: 142 [*Cardium*]. Recent; Disko Island, southwestern Greenland. Depository: unknown. Synonym of *Ciliatocardium ciliatum* (Fabricius, 1780).

icelandicum Reeve, 1845: sp. 54, pl. 11 [*Cardium*]. Recent; Iceland. Erroneously pro *islandicum* Bruguière, 1789. Synonym of *Ciliatocardium ciliatum* (Fabricius, 1780).

islandicum Bruguière, 1789: 222 [*Cardium*] ex Chemnitz, 1782: 200, pl. 19, figs. 195, 176, nonbinom. (Official index . . ., 1958: 5, Direction 1). Recent; Iceland. Depository (syntypes): Universitetets Zoologiske Museum,

Kφbenhavn, Denmark, reg. no. ?. Synonym of *Ciliatocardium ciliatum* (Fabricius, 1780).

iwatense Chinzei, 1959: 125, pl. 11, figs. 9 (holotype), 10 [*Clinocardium*]. Near Ochiai, Kintaichi-mura, Ninohe District, Iwate Prefecture, Honshu; Sannohe group, Kubo Formation, Pliocene. Depository (holotype): Institute of Geology, Faculty of Science, University of Tokyo, Tokyo, Japan, reg. no. 8572.

makiyamae Kamada, 1962: 104, pl. 10, figs. 18 (holotype), 19–21 [*Clinocardium asagaiense makiyamae*]. Nabezuka, Hironomachi, Joban coal-field, Honshu; Asaga Formation, Oligocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 15800. For taxonomic notes see: Kafanov, 1974a: 1470.

matchgarense Makiyama, 1934: 137, pl. 5, figs. 31 (holotype), 30 [*Cardium (Cerastoderma)*. Shore of Cape Marie, near Matchigar, Schmidt Peninsula, Northern Sakhalin; "Marie Formation" [Vengerijskaya suite], Upper Oligocene. Depository (holotype): Institute of Geology and Mineralogy, Kyoto University, Kyoto, Japan, reg. no. 100007.

mutuense Nomura & Hatai, 1936: 279, pl. 33, fig. 11 [*Cardium (Clinocardium)*]. Komatazawa, Aiuti-mura, Mutu Province, Honshu; Isomatsu Formation, Oligocene. Depository (holotype): Saito Ho-on Kai Museum, Sendai, Japan, reg. no. 8799.

padimeicum Merklin & Zarkhidze in Merklin, Zarkhidze & Ilyina, 1979: 44, pl. 7, figs. 10 (holotype), 11 *[Clinocardium ciliatum]*. Nadejtyvis River, Padimejskaya suite, Pleistocene. Depository (holotype): Paleontological Institute of the U.S.S.R. Academy of Sciences, Moscow, U.S.S.R., reg. no. 2700/76. Synonym of *Ciliatocardium ciliatum* (Fabricius, 1780).

ciliatum pubescens Couthouy, 1838: 61, pl. 3, fig. 6 [*Cardium pubescens*]. Recent; Massachusetts Bay. Depository: unknown.

? sachalinense Khramova, 1962: 437, pl. 1, figs. 6 (holotype), 7 [*Clinocardium*]. Keton River, Poronajskij District, South Sakhalin; lower part of Kurasijskaya suite, Middle Miocene. Depository (holotype): All-Union Oil Research Geological Institute, Leningrad, U.S.S.R., reg. no. 659/46.

salvationemense Lautenschläger in Khramova, 1962: 438, pl. 1, figs. 8 (holotype), 9–12 [*Clinocardium*]. Cape Spassennyj, Tatar Strait coast, Alexandrovskij District, Western Sakhalin; Gennojshinskaya suite, Oligocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 84/6197. Synonym of *Ciliatocardium asagaiense* (Makiyama, 1934).

schmidti Khramova, 1962: 436, pl. 1, figs. 1 (holotype), 2, 3 [*Clinocardium*]. North coast of Schmidt Peninsula west of Matchigar Lake, Northern Sakhalin; middle part of Matchigarskaya suite, Upper Oligocene. Depository (holotype): All-Union Oil Research Geological Institute, Leningrad, U.S.S.R., reg. no. 659/24.

shinjiense Yokoyama, 1923: 7, pl. 2, figs. 6a–b [*Cardium*]. Fujina, Tamayu-mura, Yatsuka District, Shimane Prefecture, Honshu; Fujina Formation, Middle Miocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?

snatolense Krishtofovich, 1947: 74, pl. 8, fig. 7 [*Cardium (Acanthocardia) snatolensis*]. Sea cliff southwest of the mouth of the Ilinushka River, Western Kamchatka; upper part of Tigiljskaya series, Oligocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 78/5610.

tigilense Slodkewitsch, 1938: 380, pl. 74, figs. 10, 10a [*Laevicardium(?)*]. Near the mouth of the Polovinnaya River, western Kamchatka; lower part of Kavranskaya suite, Upper Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 914/5060.

uyemurai Kanehara, 1937: 175, text-figs. 6–8 [*Cardium (Cerastoderma)*]. "Great Fuhdji, North Karafto" [Boljshaya Khudi River, Pogranichnyj District], southeastern part of North Sakhalin; "sandy shale of the Congi Series" [Pliocene]. Depository: "Geological Survey of Japan."[4]

yakatagense Clark, 1932: 813, pl. 18, fig. 8 [*Cardium (Cerastoderma)*], Yakataga District (about 60°N), Gulf of Alaska; upper part (?) of the Poul Creek Formation, Lower Miocene (?). Depository (holotype): Museum of Paleontology, University of California, Berkeley, U.S.A., reg. no. 30384.

yamasakii Makiyama, 1934: 138, pl. 5, figs. 23 (holotype), 24 [*Cardium (Cerastoderma)*]. Shore of Cape Marie, near Matchigar, Schmidt Peninsula, northern Sakhalin; "Marie Formation" [Vengerijskaya suite], Upper Oligocene. Depository (holotype): Insti-

[4]According to Hatai & Nisiyama (1952), all collections from the Geological Survey of Japan were totally destroyed during the World War II.

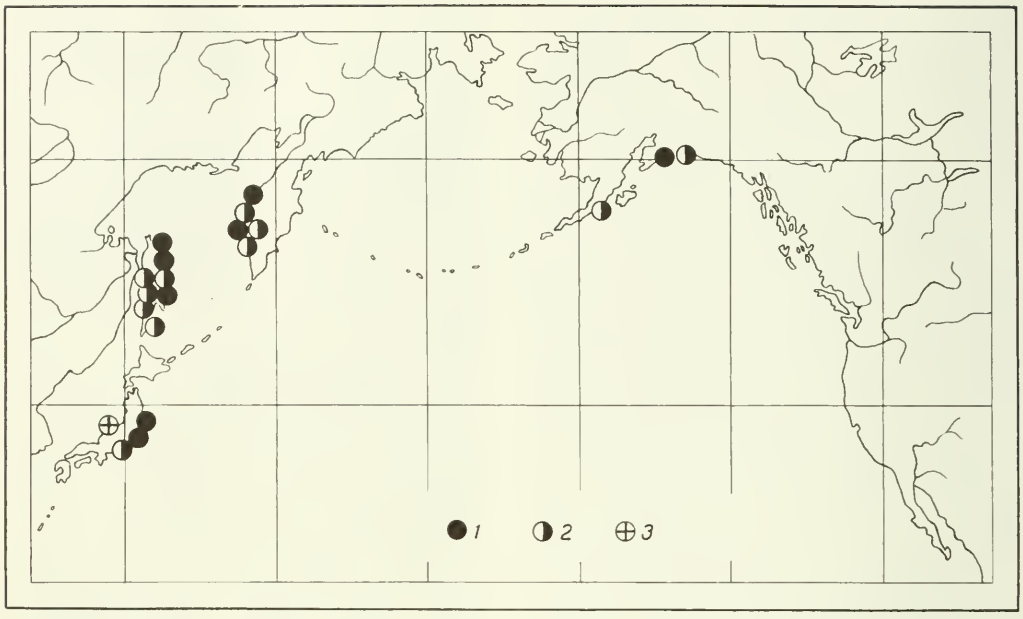

FIG. 8. Geographical and geological distribution of *Profulvia*. 1—Oligocene; 2—Miocene; 3—Pliocene.

tute of Geology and Mineralogy, Kyoto University, Kyoto, Japan, reg. no. 100005.

Tribus Profulviini Kafanov in Kafanov & Popov, 1977

Kafanov & Popov, 1977: 62

Shell carinate, gaping posteriorly or at both ends. Radial ribs well developed, convex anteriorly, curved on posterior part of valve. Beaks nearly orthogyrate, weakly prosogyrate or opisthogyrate.

Oligocene-Pliocene; northwestern Pacific and Alaska (Fig. 8).

Genus *Profulvia* Kafanov, 1976

Profulvia Kafanov, 1976: 111.

Type-species: *Papyridea harrimani* Dall, 1904; Unga conglomerate, lower part of Middle Miocene, Popov Island, Alaska Peninsula (original designation).

Shell medium-sized or fairly large (about 100 mm and more), elongate-ovate, truncated, variably inequilateral, moderately convex, frequently carinate, with gape at posterior or both ends. Beaks relatively low, obtuse, weakly prosogyrate, nearly orthogyrate or opisthogyrate. Ribs about 30–65 in number. Ribs straight, narrow and low on the anterior valve surfaces, more curved posteriorly. Ribs convex anteriorly (Fig. 4b); their height and width increase and flattened intercostal spaces become deeper posteriad. Ribs frequently reduced on the posterior slope. Ribs rounded or triangular in cross-section, or combination of these two types observed: 1) ribs are low and rather rounded in cross-section on the anteror valve surface and 2) ribs are high, irregularly triangular with abrupt posterior wall and more sloped anterior wall on the posterior valve surfaces. Ridges of ribs with numerous commarginal lines, wrinkles and growth lines; weak nodes occur where growth lines cross costal crests. Dental margin weakly curved. Paired cardinal teeth small and straight in both valves; lateral teeth usually single. Lunula and escutcheon areas weak. Internal valve surfaces or at least their ventral part with distinct indentations and ventral margin serrated.

Geographical and geological distribution as in the tribus (Fig. 8).

Key to the species

1. Average height/length ratio about 0,83 or less ..... 2.
   Average height/length ratio more than 0,84 ..... 9.
2. Maximum size of adult shell less than 70 mm ..... 3.
   Maximum size of adult shell more than 70 mm ..... 8.
3. Shell inequilateral (beaks near the anterior 0,37–0,38) *sertunayana* (Slodkewitsch, 1938).
   Shell subequilaeral (beaks near the anterior 0,42–0,44) ..... 4.
4. Ribs 38 or fewer ..... 5.
   Ribs more than 38 ..... 6.
5. Average height/length ratio about 0,81; ribs 36–37 ..... *angulata* (Slodkewitsch, 1938).
   Average height/length ratio about 0,75; ribs 32–33 .... *noyamiana* (Slodkewitsch, 1938).
6. Average height/length ratio about 0,82–0,83; ribs 40–45 ..... *utcholokensis* (Slodkewitsch, 1938).
   Average height/length ratio about 0,70–0,77; ribs more than 45 ..... 7.
7. Average height/length ratio about 0,70; maximum size of adult shell about 55 mm ..... *kurodai* (Hatai & Nisiyama, 1952).
   Average height/length ratio about 0,75–0,77; maximum size of adult shell about 35 mm . ..... *kovatschensis* (Ilyina, 1962).
8. Shell subequilateral (beaks near the anterior 0,41–0,42); ribs 50–60 ..... *matschigarica* (Khomenko, 1938).
   Shell strongly inequilateral (beaks near the anterior 0,32); ribs 36–40 ..... *securiformis* (Slodkewitsch, 1938).
9. Average height/length ratio about 0,90–0,92 ..... 10.
   Average height/length ratio about 0,85–0,86 ..... 11.
10. Ribs 40–45; maximum size of adult shell about 90 mm . *kipenensis* (Slodkewitsch,1938).
    Ribs 60 or more; maximum size of adult shell about 50 mm ..... *hamiltonense* (Clark, 1932).
11. Ribs about 30 in number ..... *sakhalinensis* (Slodkewitsch, 1938).
    Ribs about 40–45 in number ..... *harrimani* (Dall, 1904).

angulata Slodkewitsch, 1938 (ex Kogan, MS): 404, pl. 81, figs. 8, 8a [*Papyridea*]. Between the mouths of Noyami and Malyj Sertunaj Rivers, western Sakhalin; "Rykhlaya suite" [Sertunajskaya and Alexandrovskaya suites], lower Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 180/5294.

hamiltonense Clark, 1932: 813, pl. 18, figs. 7 (holotype), 6,10 [*Cardium (Serripes)*]. Yakataga District (about 60°N), Gulf of Alaska; Poul Creek Formation (?), Upper Oligocene(?)-Lower Miocene (Addicott, 1971; Addicott et al., 1971). Depository (holotype): Museum of Paleontology, University of California, Berkeley, U.S.A., reg. no. 30405.

harrimani Dall, 1904: 114, pl. 10, fig. 5 [*Papyridea*]. North coast of Popov Island, Alaska Peninsula; Bear Lake Formation, Unga conglomerate, lower Middle Miocene, Depository (holotype): U.S. National Museum, Washington, D.C., U.S.A., reg. no. 164867.

kipenensis Slodkewitsch, 1938: 409, pl. 82, figs. 2 (holotype), 1, pl. 83, figs. 1–3 [*Papyridea*]. 18 km from the mouth of the Snatol River, western Kamchatka; upper part of the Kavranskaya series [Upper Miocene]. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 902/5060.

kovatschensis Ilyina, 1962: 343, pl. 2, figs. 8, 8a [*Papyridea*]. Utkholok Cape, western Kamchatka; "Tufogennyj horizon," lower part of Voyampoljskaya series, Oligocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 121/6068.

kurodai Hatai & Nisiyama, 1952: 105 [*Papyridea (Fulvia)*] pro *Papyridea (Fulvia) nipponica* Yokoyama, 1926c: 294, pl. 34, fig. 16 non 1924: 17, pl. 3, figs. 3, 4. Sawane, Sado Island, Niigata Prefecture, Honshu; Sawane formation, Lower Pliocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?.

matschigarica Khomenko, 1938: 47, pl. 7, figs. 5 (lectotype), 6, 7, pl. 8, fig. 6, pl. 9, fig. 7 [*Papyridea*]. Between the Marie Cape and Matchigar Lake, Schmidt Peninsula, northern Sakhalin; lower part of the Machigarskaya

suite, Oligocene. Depository (lectotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 81/5044. For figure of lectotype see: Slodkewitsch, 1938, pl. 84, fig. 2.

nipponica Yokoyama, 1924: 17, pl. 3, figs. 3, 4 [*Papyridea (Fulvia)*]. Tatsuta coal-field, Futaba District, Fukushima Prefecture, Honshu; Asagai Formation, Oligocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?. Following Hatai & Nisiyama (1952) and Makiyama (1957), the author considers this form a synonym of *Profulvia harrimani* (Dall, 1904).

noyamiana Slodkewitsch, 1938 (ex Kogan, MS): 413, pl. 86, figs. 3 (holotype), 2 [*Papyridea*]. Between the mouths of Noyami and Malyj Sertunaj Rivers, western Sakhalin; "Rykhlaya suite" [Sertunajskaya and Alexandrovskaya suites], lower Middle Miocene. Depository (holotype): Central Research Geogical Prospecting Museum, Leningrad, U.S.S.R., reg. no. 181/5294.

sakhalinensis Slodkewitsch, 1938 (ex Kogan, MS): 412, pl. 86, fig.1 [*Papyridea*]. Between the mouths of Noyami and Malyj Sertunaj Rivers, western Sakhalin; "Rykhlaya suite" [Sertunajskaya and Alexandrovskaya suites], lower Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 182/5294.

securiformis Slodkewitsch, 1938: 411, pl. 85, fig. 1 [*Papyridea*]. Kovachina Bay, western Kamchatka; lower part of Kavranskaya series, Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 899/5060.

sertunayana Slodkewitsch, 1938 (ex Kogan, MS): 405, pl. 82, figs. 3, 3a [*Papyridea*]. Between the mouths of Noyami and Malyj Sertunaj Rivers, Western Sakhalin; "Rykhlaya suite" [Sertunajskaya and Alexandrovskaya suites], lower Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 185/5294.

utcholokensis Slodkewitsch, 1938: 403, pl. 82, figs. 6 (holotype), 4, 5 [*Papyridea*]. Utcholok Cape, western Kamchatka; lower part of Vayampoljskaya series, Oligocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 911/5060.

Tribus Serripedini Kafanov, 1975

Kafanov, 1975: 147.

Radial ribs obsolete or absent but their traces can usually be observed on the posterior and rarely on the anterior valve surfaces. Hinge weak due to reduction of cardinal teeth.

Early Oligocene-Recent; northwestern Pacific south to south Honshu and northeastern Pacific south to Puget Sond, Arctic Seas and North Atlantic (south to Cape Cod, Iceland and south Norway; in later Pliocene and Early Pleistocene to England and to the Netherlands) (Figs. 9, 10).

Genus *Serripes* Gould, 1841 ex Beck, MS

Aphrodite Lea, [1837]: 111 non Leske, 1775, nec Link, 1807 (pro *Aphrodita* Linne, 1758), nec Hübner, [1819], nec Lendenfeld, 1886;

Aphrodita Leach in Sowerby, 1839: 70 (pro *Aphrodite* Lea, 1837 non Linne, 1758);

Acardo Swainson, 1840: 374 non Lamarck, 1799, nec Roissy, 1805, nec Mühlfeldt, 1811, nec Menke, 1828, nec Herrmannsen, [1846];

Serripes "Beck" Gould, 1841: 93.

Type-species: *Cardium groenlandicum* Bruguière, 1789; Recent, Greenland (by monotypy).

Shell medium-sized or fairly large (to 90 mm and more), flattened, oblong-elliptical or truncate-trigonal, variously inequilateral; as a rule, anterior and broader than posterior one. Posterodorsal margin smoothly joined with the posterior valve margin. Carina on the posterior valve surface obsolete. Beaks moderately prosogyrate or nearly orthogyrate. Radial ribs almost entirely reduced. Hinge strongly reduced, frequently teeth completely absent. Bases of the anterior lower lateral teeth lie on outer side of the internal branches of hinge margin (Fig. 3a). Distal part of foot with longitudinal row of crests or denticles, ventral sulculus absent. Labial palps long and nearly equal in length to inner demibranch.

Geographical and geological distribution as in the tribus (Fig. 9).

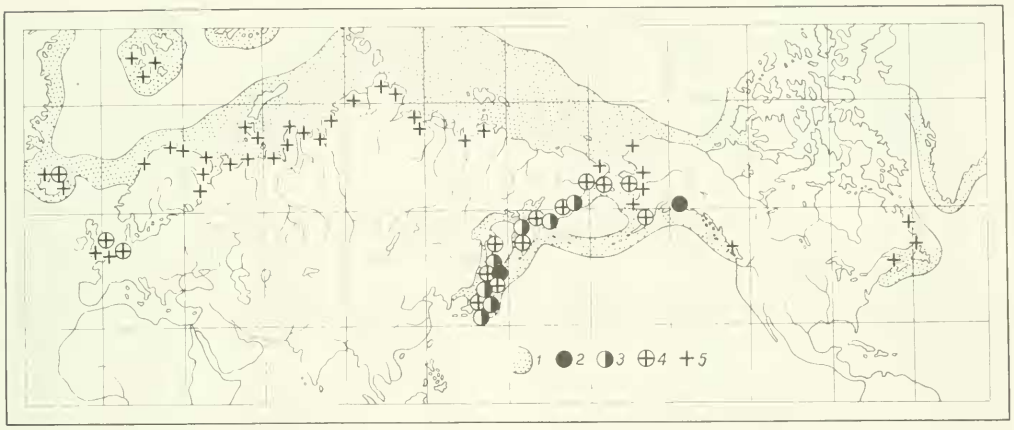

FIG. 9. Geographical and geological distribution of *Serripes*. 1—Recent. 2—Oligocene; 3—Miocene; 4—Pliocene; 5—Pleistocene.

Key to the species and subspecies

1. Traces of radial ribs well developed on the medial valve surfaces ..... *shiobaraensis* Noda, 1962.
   Traces of radial ribs not developed on the medial valve surfaces ..... 2.
2. Posterior valve margin almost straight; cardinal teeth not reduced ..... *groenlandicus fabricii* (Deshayes, 1855).
   Posterior valve margin variously curved; cardinal teeth variously reduced ..... 3.
3. Average length of adult shell more than 100 mm; shell much swollen; traces of radial ribs observed only on the anterior valve surfaces ..... *expansus* Hirayama, 1954.
   Average length of adult shell less than 100 mm; shell variously inflated; traces of radial ribs present, as a rule, on the posterior valve surfaces ..... 4.
4. Height/length ratio more than 0,96 ..... 5.
   Height/length ratio less than 0,95 ..... 9.
5. Average height/length ratio about 1,20 ..... *muraii* Noda & Tada, 1968.
   Average height/length ratio about 0,99–1,10 ..... 6.
6. Maximum size of adult shell about 95 mm; shell rather inequilateral (beaks near the anteror 0,41–0,42) ..... *kamtschaticus* Ilyina, 1963.
   Maximum size of adult shell about 60 mm; shell subequilateral or nearly equilateral .. 7.
7. Shell nearly equilateral (beaks near the anterior 0,48); average height/length ratio about 1,00 ..... *hataii* Noda, 1962.
   Shell subequilateral (beaks near the anterior 0,44–0,46); average height/length ratio about 1,10 ..... 8.
8. Shell trigonal in outline ..... *triangularis* Noda, 1962.
   Shell rounded ..... *nodai* Kafanov nom. nov.
9. Average height/length ratio more than 0,90 ..... 10.
   Average height/length ratio less than 0.90 ..... 11.
10. Shell inequilateral (beaks near the anterior 0,39–0,40); average length of adult shell about 85 mm ..... *ochotensis* Ilyina, 1963.
    Shell rather inequilateral (beaks near the anterior 0,42); average length of adult shell about 50 mm ..... *squalidus* (Yokoyama, 1924).
11. Average height/length ratio about 0,75; maximum size of adult shell about 25 mm ..... *uvutschensis* Ilyina, 1963.
    Average height/length ratio more than 0,78; maximum size of adult shell more than 40 mm ..... 12.

12. Shell strongly inequilateral (beaks near the anterior 0,37–0,38) ... *japonica* Noda, 1962.
Shell subequilateral or nearly equilateral (beaks near the anterior 0,44–0,48) ..... 13.
13. Average height/length ratio about 0,87–0,88; shell subequilateral (beaks near the anterior 0,44–0,45) ..... *groenlandicus* (Bruguière, 1789).
Average height/length ratio about 0,80–0,81; shell nearly equilateral (beaks near the anterior 0,48) ..... *laperousii* (Deshayes, 1839).

Described taxa

album Verkrüzen, 1877: 53 [*Cardium (Aphrodite) groenlandicum* var.]. Recent; Newfoundland Bank. Depository: unknown. Synonym of *Serripes groenlandicus groenlandicus* (Bruguière, 1789) or *Serripes groenlandicus fabricii* (Deshayes, 1854).

boreale Reeve, 1845: sp. 131, pl. 22 [*Cardium*] non Broderip & Sowerby, 1829: 369. Recent; Greenland. Depository (holotype): British Museum (Natural History), reg. no. 1879.2.26.235. Synonym of *Serripes groenlandicus* (Bruguière, 1789).

columba Lea, 1834: 111, pl. 18, fig. 54 [*Aphrodite*]. Type-locality not given, nor was it given subsequently; Lea listed only "Hab . . ."; on p. 111–112 under Remarks he said: "Its habitat I am not acquainted with, having purchased my specimens at a dealer's in Europe, who could not inform me from what country they came." Depository: unknown. Synonym of *Serripes groenlandicus groenlandicus* (Bruguière, 1789).

edentulum Montagu, 1808: 29 [*Cardium edentula*] non Fleming, 1813: 92 nec Deshayes, 1838: 57, pl. 3, fig. 3–6 [*Cardium*]. Recent; "on the shore near Portsmouth, after a storm." Depository: Exeter Museum, Exeter, Great Britain (?). Synonym of *Serripes groenlandicus groenlandicus* (Bruguière, 1789).

expansus Hirayama, 1954: 66, pl. 4, figs. 1 (holotype), 2 [*Serripes*]. Nanatsuishi, Oyamada-shimogo, Oyamada-mura, Tochigi Prefecture, Honshu; Kobana Formation, Lower Miocene. Depository (holotype): Tokyo University of Education (Kyoiku Daigaku), Tokyo, Japan, reg. no. 10136.

groenlandicus fabricii Deshayes, 1855: 333 [*Cardium fabricii*]. Recent; Iceland. Depository (holotype): Zoological Institute of the U.S.S.R. Academy of Sciences, Leningrad, U.S.S.R., reg. no. 1/13460. For figure of holotype, see Middenforff, 1849: pl. 16, figs. 6, 7.

fujinensis Yokoyama, 1923: 5, pl. 2, figs. 2a–b [*Mactra*]. Matsue, Fujina, Tamayumura, Yatsuka District, Shimane Prefecture, Honshu; Fujina Formation, Middle Miocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ? Unlike Noda (1962), the author considers this form a synonym of *Serripes groenlandicus* (Bruguière, 1789) rather than of *S. laperousii* (Deshayes, 1839) because of the general valve outlines, their considerable convexity and significantly elevated beaks.

groenlandicus Bruguière, 1789: 222 ex Chemnitz, 1782: 202, pl. 19, fig. 198, nonbinom. (see: Official Index . . , 1958: 5, Direction 1) [*Cardium*]. Recent; [southeastern] Greenland (here limited; Chemnitz reports that the majority of representatives of this species was collected for him from Julianehob). Depository (possible syntypes): Universitetets Zoologiske Museum, Kϕbenhavn, Denmark, reg. nos. ? Recent records: North Pacific (south to central parts of Honshu, Korea?, Peter the Great Bay, Aleutian and Commander Islands and Puget Sound, Washington), North Atlantic (south to Iceland, southern Greenland and Cape Cod, Massachusetts) and epicontinental Arctic Seas. Fossil records: Miocene Echinskaya suite of Chukotka, Yakataga formation of Alaska, Undal-Umenskaya suite of Koryak Plateau, Pestrotsvetnaya and Yunjunjvayamskaya suites of Keraginskij Island, Ilyinskaya, Etolonskaya, Kuluvenskaya, Goryachikh Klyuchej and Nachikinskaya suites of Kamchatka, Alekhinskaya, Kamujskaya and Okruglovskaya suites of Kurile Islands, Uglegorskaya, Sertunajskaya, Uranajskaya, Borskaya, upper and middle parts of Maruyamskaya, Ausinskaya, Kurasijskaya and Okobykajskaya suites of Sakhalin, Okada, Chijubetsu, Magaribuchi, Sin-uryu, Wakkanai formations of Hokkaido, Kobana, Fujina, Kurosawa, Kanomatazawa, Ogino, Takahoko, Hongo and Utsutoge formations of Honshu; Pliocene Pinakuljskaya suite of Chukotka, upper part of Limimtevayamskaya and Ustj-Limimtevayamskaya suites of Karaginskij Island, Gavanskaya suite of Kamchatka, Golovinskaya, Parusnaya and Okeanskaya suites of Kurile Islands, upper part of Maruyamskaya, Mayamrafskaya, Matitukskaya and Pomyrskaya suites of Sakhalin, Gobansoyama, Ebishima, Rigashigawa, Sizun and Takinoe formations

of Hokkaido and Northern Honshu; Pliocene and Plio-Pleistocene of Iceland (Tjornes Crag, zone of *Serripes groenlandicus*), England (Red Crag) and the Netherlands (Dutch Icenian); Pleistocene sediments of Arctic and Subarctic regions of the Northern Hemisphere.

? haboroensis Yokoyama, 1927b: 198, pl. 52, figs. 3 (lectotype; designated by Hatai & Nisiyama, 1952: 86), 4 [*Mactra*]. Sankebetsu, off Shinkukaku, Haboro-machi, Tomamae District, Teshio Province, Hokkaido; Chikubetsu Formation, Lower Miocene. Depository (lectotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?. Shell form closely resembles that of *Serripes groenlandicus* (Bruguière, 1789). The author cannot refer this species with confidence to Serripedini for lack of data on hinge structure.

hataii Noda, 1962: 224, pl. 37, fig. 3 [*Serripes*]. Iwaigawa, Kamikurosawa, Hagihana-mura, Nishiiwai District, Iwate Prefecture, Honshu; lower part of the Nishikurosawa Formation, Lower Miocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 74593.

japonica Noda, 1962: 225, pl. 39, fig. 4 [*Serripes*]. Mukai, Sakekawa, Mogami District, Yamagata Prefecture, Honshu; Sakekawa Formation, Lower Pliocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 78680.

kamtschaticus Ilyina, 1963: 102, pl. 43, figs. 2 (holotype), 3 [*Serripes*] sea cliff between the Moroshechnaya and Kovachina Rivers, western Kamchatka; Etolonskaya suite, upper Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 24/96338.

laperousii Deshayes, 1839: 360; 1841b: pl. 48 [*Cardium*]. Recent; Kadjak Island, Gulf of Alaska (type-locality here designated; in original description as type-locality are mentioned "Mers de Californie" but this species is absent from the coast of California). Depository: unknown. As fossil it was recorded from Middle and Upper Miocene and Pliocene of northeastern and north Honshu and Hokkaido (reviewed by Noda, 1962), from Upper Miocene and Pliocene of Sakhalin and Kurile Islands, but it should be noted that there is much evidence that the fossil representatives of this species in fact belong to *Serripes groenlandicus* (Bruguière, 1789) and to other species of the genus. It is unknown in Neogene deposits of the northeastern Pacific.

muraii Noda & Tada, 1968: 202, pl. 22, fig. 22 [*Serripes*]. Small tributary of the Kakkonda River, about 4 km NNW of the Takinoue Spa, Shizukuishi-machi, Iwate Prefecture, Honshu; Yamatsuda Formation, upper Middle Miocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 88058.

nodai Kafanov nom. nov. pro *Cardium pauperculum* Yokoyama, 1923: 6, pl. 1, figs. 2a–c non Meek, 1871: 306 [*Serripes*]. Kami-Ichiba, Shimane Prefecture, Honshu; Fujina Formation, Middle Miocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ? For taxonomic notes see: *pauperculum* Yokoyama, 1923.

ochotensis Ilyina, 1963: 102, pl. 42, figs. 2 (holotype), 1 [*Serripes*]. Sea cliff between the Etolona River and Nepropusk Cape; Etolonskaya suite, Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 248/6338.

pauperculum Yokoyama, 1923: 6, pl. 1, figs. 2–c non Meek, 1871: 306, nec Yokoyama, 1925c: 121, pl. 14, figs. 12, 13 nec 1926b, 243, pl. 30, fig. 3 [*Cardium*], Kami-Ichiba, Shimane Prefecture, Honshu; Fujina Formation, Middle Miocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ? Following Noda (1962), Keen (1973) considers this species to be a synonym of *Serripes groenlandicus* (Bruguière, 1789). Yokoyama described and figured three different forms called *Cardium pauperculum*: 1) the holotype, a specimen which slightly resembles *Serripes hataii* Noda, 1962 and is much different in shell outlines from all Recent and fossil *Serripes groenlandicus* (Bruguière, 1789); 2) a specimen from the Oligocene Akahira Beds of Central Honshu described and figured by Yokoyama (1925c, 121: pl. 14, figs. 12, 13) for which Hatai & Nisiyama (1952: 39) suggest a new name, *Cardium arakawaense*; 3) a specimen from the Upper Miocene Wakkanai Formation of southwestern Honshu (Yokoyama, 1926b: 243, pl. 30, fig. 3) which really may be identified with *Serripes groenlandicus* (Bruguière, 1789). Noda (1962) in comparing *Cardium pauperculum* Yokoyama with *Serripes groenlandicus* (Bruguière, 1789) apparently took into account the third form mentioned above, because he cites the name in Yokoyama's paper of 1926 in synonymy with *Serripes groenlandicus* (Bruguière, 1789), but he does not mention the original description and figure of *Cardium pauperculum*

Yokoyama, 1923. Both Hatai and Nisiyama (1952) do not give it. According to the author the information does not justify the recognition of *Cardium pauperculum* Yokoyama, 1923 as a synonym of *Serripes groenlandicus* (Bruguière, 1789) and the species can retain its rank of an independent species. However owing to the presence of an older homonym, *Cardium pauperculum* Meek, 1871, *pauperculum* Yokoyama, 1923 is given the new name *Serripes nodai* in honour of the Japanese paleontologist Prof. Hiroshi Noda.

protractus Dall, 1900: 1112 [*Serripes groenlandicus* var.]. Recent; type-locality not given. Depository: unknown. Invalid name as nomen infrasubsp. s.s.

radiata Donovan, 1803: pl. 161 et text, non Spengler, 1802: 107 [*Mactra*]. Recent; "Langston Beach, near Portsmouth, after a severe storm . . ." Depository: unknown. Synonym of *Serripes groenlandicus groenlandicus* (Bruguière, 1789).

shiobaraensis Noda, 1962: 228, pl. 39, fig. 5 [*Serripes*]. Cliff facing the Hokigawa Electric Power Station along the Hoki River, Sekiya, Shiobara-machi, Shioya District, Tochigi Prefecture, Honshu; Kanomatazawa Formation, Middle Miocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Sendai, Japan, reg. no. 78587.

squalidus Yokoyama, 1924: 16, pl. 3, figs. 1, 1a [*Cardium (Laevicardium)*]. Dodaira, Misawa, Nakoso-shi, Fukushima Prefecture, Honshu; Iwaki Formation, Oligocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?

titthus Krishtofovich, 1969: 192, pl. 4, figs. 4 (holotype), 5, 9, 12, 14 [*Serripes*]. Near the mouth of the Talovaya River, Kronotskij Reservation, East Kamchatka; Tyushevskaya suite, Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R., reg. no. 62/6780. Synonym of *Serripes groenlandicus* (Bruguière, 1789).

triangularis Noda, 1962: 229, pl. 39, figs. 2 (holotype), 3 [*Serripes*]. Itanoki-sawa, Arakimura Mogami District, Yamagata Prefecture, Honshu; Mitsumori Formation, Upper Miocene. Depository (holotype): Saito Ho-on Kai Museum, Sendai, Japan, reg. no. 8410.

unciangulare Khomenko, 1931: 75, pl.10, fig. 21 [*Cardium groenlandicum unciangulare*]. Boljshoj Garomaj River, east Kamchatka; "Nadnutovskaya" suite, Pliocene. Synonym of *Serripes groenlandicus* (Bruguière, 1789) as shown by original description: "Form described here represents the extreme degree of inequilaterality of lower forms of *Cardium groenlandicum*. . . ." Moreover, according to the faunal lists in Khomenko's paper it frequently occurs together with the typical *Serripes groenlandicus* (Bruguière, 1789).

uvutschensis Ilyina, 1963: 76, pl. 25, fig. 5 [*Serripes (?)*]. Cliff of the Kovachina Bay near the mouth of Moroshechnaya River; Ilyinskaya suite, Middle Miocene. Depository (holotype): Central Research Geological Prospecting Museum, Leningrad, U.S.S.R. reg. no 103/6338.

Genus *Yagudinella* Kafanov, 1975

Yagudinella Kafanov, 1975: 147.

Type-species: *Cardium (Serripes) notabile* Sowerby, 1915; Recent, Wakasa Bay, Honshu (original designation).

Shell medium-sized or fairly large (to 100 mm and more), convex, truncated, obviously inequilateral. Anterior end much narrower than posterior one. Posterodorsal margin passes into posterior valve margin at an angle. Posterior valve surface, as a rule, with pronounced carina. Beaks strongly inclined forward and prosogyrate. Clear traces of the radial ribs on the anterior and posterior valve surfaces. Cardinal teeth somewhat reduced. Bases of the anterior lower lateral teeth lie on the ventral side of anterior part of hinge margin and their proximal parts extended posterodorsally toward beaks (Fig. 3b). Distal part of foot with longitudinal row of closely spaced combs but not denticles, which are high, inflated on the sides; ventral sulculus absent. Labial palps long and near equal in length to the inner demibranch.

Middle Miocene-Recent; northwestern Pacific (south to southwestern Honshu).

Key to the species and subspecies

1. Shell hatchet-shaped in outline ..... *yokoyamai* (Otuka, 1935).
   Shell triangular in outline ..... 2.
2. Shell strongly inequilateral (beaks near the anterior 0,38–0,39) ..... 3.
   Shell subequilateral (beaks near the anterior 0,41–0,48) ..... 4.

3. Average height/length ratio about 0,94 ..... *makiyamai makiyamai* (Yokoyama, 1928).
   Average height/length ratio about 0,83 ..... *makiyamai nigamiensis* (Noda, 1962).
4. Average height/length ratio about 1,00; shell almost equilateral (beaks near the anterior 0,48) ..... *notabilis notabilis* (Sowerby, 1915).
   Average height/length ratio about 0,81–0,82; shell subequilateral (beaks near the anterior 0,41) ..... *notabilis nomurai* (Otuka, 1943).

Described taxa

makiyamai Yokoyama, 1928: 360, pl. 69, fig. 3 [*Mactra*]. Nagaoka, River side at Hanzogane, Hanzogane-mura, Koshi District, Niigata Prefecture, Honshu; Ushigakubi Formation, Upper Miocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ?

makiyamai nigamiensis Noda, 1962: 227, pl. 39, figs. 1a–c [*Serripes*]. Nigami, Ooshima-mura, Higashikubiki District, Niigata Prefecture, Honshu; Shiiya Formation, Upper Miocene. Depository (holotype): Institute of Geology and Paleontology, Tohoku University, Japan, reg. no. 78684.

notabilis nomurai Otuka, 1943; 56, pl. 3(2), fig. 10 [*Serripes*]. Nakanango, Saunai-mura, Hiraga District, Akita Prefecture, Honshu; Kurosawa Formation, Middle and Upper Miocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. ? Noda (1962) considers this form identical with *Serripes notabilis* (Sowerby, 1915). However, the numerous Recent and fossil specimens of the latter species are distinguished by their more angulate outlines and more truncated valves. The author there-

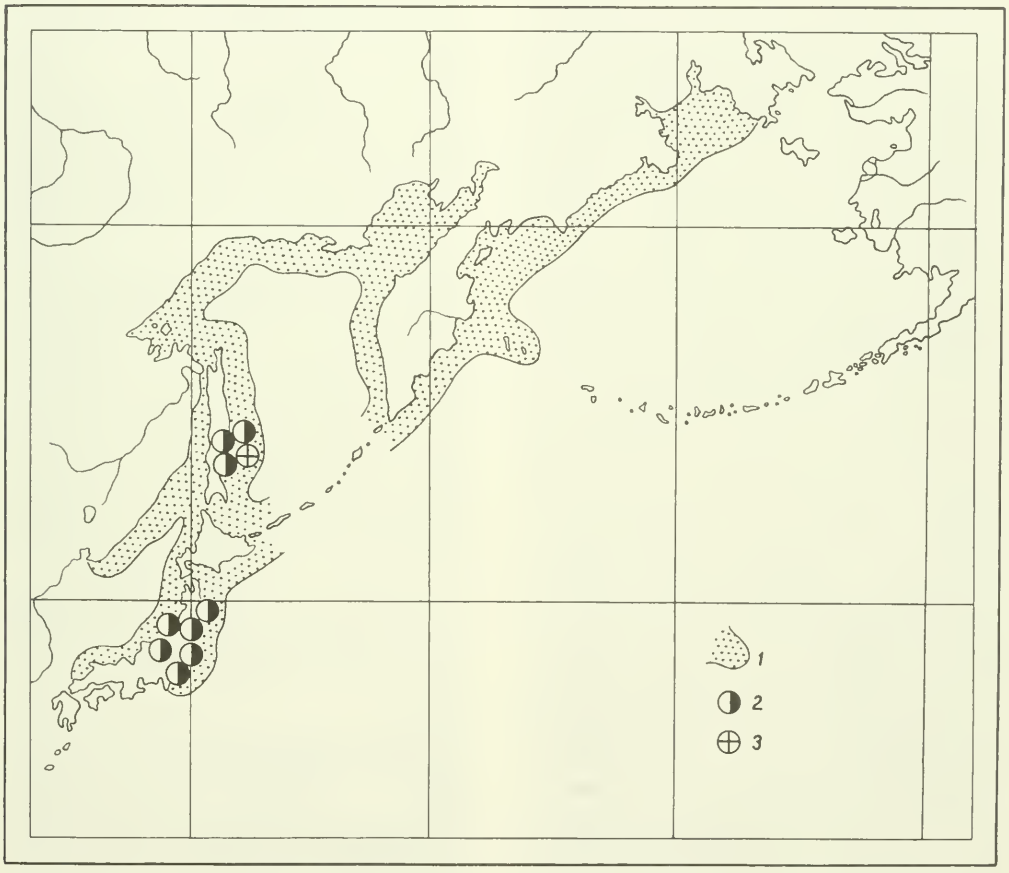

FIG. 10. Geographical and geological distribution of *Yagudinella*. 1—Recent; 2—Miocene; 3—Pliocene.

fore finds it quite possible that this form should retain its rank of a separate subspecies.

notabilis Sowerby, 1915: 169, pl. 10, fig. 9 [*Cardium (Serripes)*]. Wakasa Bay, Honshu; Recent. Depository (holotype): British Museum (Natural History), London, Great Britain, reg. no. 1919.12.31.38. Recent distribution: see Fig. 10. Fossil records reviewed by Noda (1962).

yokoyamai Otuka, 1935: 603, pl. 2, fig. 3, 4 (holotype), 5, 6 [*Serripes*]. Ogino, Yamanogomura, Yama District, Fukushima Prefecture, Honshu; Hitosao Formation, Middle and Upper Miocene. Depository (holotype): Geological Institute, University of Tokyo, Tokyo, Japan, reg. no. 2531.

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Абстракт

Система и состав подсемейства Clinocardiinae Kafanov, 1975 (Bivalvia, Cardiidae)

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При ревизии кайнозойских Cardioidea автор установил новое подсемейство Clinocardiinae. В данной работе обсуждается история изучения клинокардиин, объем и состав подсемейства и его положение в системе Carddiidae. Даны определительные таблицы для триб,

родов, видов и подвидов, а также детальные диагнозы для подсемейства, триб, родов и подродов. Прилагаемый каталог содержит все описанные до сих пор таксоны видового ранга со ссылками на оригинальные описания, указаниями на типовые местонахождения и места депонирования типового материала. В несбходимых случаях даны таксономические замечания. Для Cardium pauperculum Yokoyama, 1923 non Meek, 1871 предложено новое название: Serripes nodai nom.nov.